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TRANSACTIONS

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VOL. XXXII.

THE FOSSIL SUINA OF SOUTH AFRICA.

By H. B. S. Cooke, Department of Geology, University of the Witwatersrand, Johannesburg.

(With nineteen Text-figures.)

(Read May 15, 1946.)

Introduction.

The Artiodactyla as a whole have provided a very considerable body of fossil material from the limestone caves and the superficial deposits of South Africa and a number of supposedly extinct species have been described from time to time. Of these species a large proportion are referred to various members of the pig family and, indeed, the Suina have furnished a variety of valuable and interesting specimens which have been widely discussed.

In a most valuable paper, presented to the Royal Society of South Africa, Professor J. C. Middleton Shaw (1939) gave the results of comprehensive investigations upon the characters of the third molar of the wart-hogs and he attempted to clarify the confusion of specific nomenclature of the extinct members of this family. While following Shaw completely in his work on the recent species, the present writer and Dr. L. H. Wells have considered it necessary to re-distinguish certain extinct species which Shaw included with the living forms (Wells and Cooke, 1942; Cooke and Wells, 1945). In consequence it now appears that a fresh discussion of the extinct forms is necessary before further material can profitably be described.

Shaw's work was confined almost entirely to the incisors and third molars of the wart-hogs but the remaining teeth, also found as fossils, were

not described. Furthermore, no revision of the fossil hippopotamidae has hitherto been attempted and the teeth of the bush-pig have not previously been discussed, so that the present state of nomenclature amongst the Suina is somewhat confused and unsatisfactory. It is accordingly proposed to set out here a new synonymy according to the ideas of the present writer and to take the opportunity of giving brief systematic descriptions of the species now recognised in order to facilitate the identification and descriptions of fossil material in the future. It must be pointed out that, despite the points wherein the writer differs from Shaw as far as the wart-hogs are concerned, the present essay would not have been possible without the basis of Shaw's comparative work upon which to found it.

Abbreviations for Museum Numbers.

In the descriptions which follow the catalogue numbers assigned to the various specimens discussed are noted in the descriptions, preceded by an abbreviation indicating the Museum concerned. The following are the abbreviations used:—

Alb. Mus. = Albany Museum, Grahamstown.
Arch. Sur. = Archaeological Survey Museum, University of the Witwatersrand, Johannesburg.
M.M.K. = McGregor Memorial Museum, Kimberley.
Nas. Mus. = Nasionale Museum, Bloemfontein.
S.A. Mus. = South African Museum, Cape Town.

Description of Species.

Section SUINA.

Family HIPPOPOTAMIDAE.

Three supposedly extinct species and two varieties of hippopotamus have been described from South Africa in addition to material referred to the living species, but the validity of any of these is doubtful. The living hippopotamus is an extraordinarily variable animal as far as size is concerned, and its dental characters are also subject to a very unusual range of variability. Undeniably extinct species of hippopotamus have been described from Central Africa, but these are not known to occur in Southern Africa. Fraas' (1907) cautious "Jedoch halte ich diese Unterscheide nicht für ausreichend zur Abtrennung eigenen Spezies, sondern möchte die pleistocäne Form vorläufig, bis weiters Funde die Entscheidung bringen, nur als eine ausserordentlich kräftige unde grosse Varietät ansehen, was durch den Beinamen *robustus* ausgedrückt werden soll" shows a very correct attitude towards hippopotamus fossils!

Genus HIPPOPOTAMUS Linnaeus.

Genotype: *Hippopotamus amphibius* Linnaeus.

Hippopotamus amphibius Linnaeus.

Hippopotamus amphibius Linnaeus, 1758: Syst. Nat., ed. 10, 1, p. 74.

Hippopotamus ponderosus Scott, 1907: Third and Final Rep. Geol. Survey Natal and Zululand, pp. 254–255, pl. xvi (1–3).

Hippopotamus amphibius var. *robustus* Fraas, 1907: Zeit. d. Deutsch. Geol. Gesell., 59, ii, pp. 238–240, pl. viii.

Hippopotamus westphali Lyle, 1931: "New Fossil Mammals and Man," pp. 13–15, pl. ii (5), iii (1 and 1*a*).

Hippopotamus amphibius var. *venteri* Lyle, 1931: Idem., p. 13, pl. iii (4, 4*a*), iv (7).

Hippopotamus helmei Lyle, 1931: Idem., pp. 13–19, pl. iii (2, 2*a*, 3 and 3*a*), iv (4–6).

The living African hippopotamus is one of the largest of existing mammals. The whole body is very massive, and the skull has a much elongated facial portion with prominent orbits and supra-orbital ridges. The mandible is large and heavy and is distinguished by the possession of a rounded descending process at its outer angle. The two jaws carry a remarkable defensive armament of exaggerated canine and incisor teeth. The female is always smaller than the male and the limits of size consequently have a much-extended range so that a large male and a small female might quite readily be mistaken for different species. The largest skull which the writer has seen measured 79 cm. in length and 47 cm. in breadth. The cheek teeth occupied 29 cm. and the lower canines were 30 to 35 cm. long. It is possible that still larger skulls may occur though the measurements given above must be near the limit. The average skull is probably about 60 cm. long, but many adult female skulls are only 50–55 cm. in length. The limits of size are thus quite abnormally large and the variation in individual characters appears equally large.

The upper jaw carries two incisors in each premaxillary, these teeth curving downwards and outwards and being quite short. They oppose the four straight lower incisors, which are considerably longer than the uppers. The central pair of lower incisors is much longer than the outer pair. The tips of both sets are obliquely abraded, the upper ones normally having the worn surface sloping from above downwards and backwards, while the lowers are worn parallel to them and thus have their abraded surfaces on the inner side. Exceptionally, however, these directions may be reversed. The upper canines likewise curve downwards and outwards and are very short, possessing the same abraded angle as the incisors.

These teeth are sub-triangular in cross-section with a wide and deep posterior longitudinal groove. The lower canines are very massive and curve in an arc of a circle with almost the whole posterior face abraded. Lower canines up to 40 inches (100 cm.) in length along the curve have been recorded, but a good average would probably be 15–20 inches (35–50 cm.). In addition to the longitudinal grooves, the canines also show transverse growth ridges of variable development. All these incisor and canine teeth are unrooted and grow continuously to offset the severe abrasion which they undergo as a consequence of the coarse diet of the animal.

The cheek teeth are arranged in a continuous row with the only gap between succeeding teeth occurring between the first and second premolars. All the premolars have a rather simple laterally compressed conical form with very small anterior and/or posterior cusps or tubercles. The first premolar, which is single rooted, is shed early in life and other (two-rooted) premolars may sometimes be shed at later stages, but not necessarily in order from front to rear so that gaps may appear in the dental series. The variability of development of the secondary cusps in these teeth is remarkable. In wear the premolars at first show a flattened area of enamel on the tip of the conical cusp, but as abrasion proceeds an irregular ring of enamel is exposed with a dentine centre. In advanced wear the whole tooth is worn to an oval enamel ring surrounding a tract of dentine.

The first and second molars are primarily divided into an anterior and a posterior pair of outer columns,* each column expanding inwards into a pair of ridges. The appearance is consequently that of an anterior and a posterior lobe each medially divided. A greatly flattened plate-like cone rises from the cingulum at the front and at the back of the tooth, reaching about one- to two-thirds the height of the main cones, the posterior plate being always the higher of the two.

The third molar is lengthened by the development of a fifth main column (or heel) more or less centrally placed behind the posterior pair. This column is flanked by lower conelets or ridges of very varying development and the posterior plate is lacking. This tooth has five roots, as against the four roots of the other molars. (It may be noted that an exceptional specimen in the South African Museum collection possesses an extra lower molar on the left side, and the morphology of this tooth is the same as that of the third molar which precedes it.) Lower third molars are longer than uppers.

In wear the main columns each show a trefoil enamel pattern which develops until the pairs of columns unite to produce two quadrilobate

* Presumably the metacone and hypocone, and the paracone and protocone of Osborn.

figures. The anterior and posterior plates form an expansion of the fourth lobe of the figure. This is seen in fig. 1, and the minor difference in third molar pattern is also to be seen in that figure.

The enamel pattern changes a good deal with wear and the breadth of the grinding surface increases progressively as abrasion proceeds. The length of the grinding surface also changes with wear, increasing at first and later decreasing, but this change is less rapid than the lateral expansion

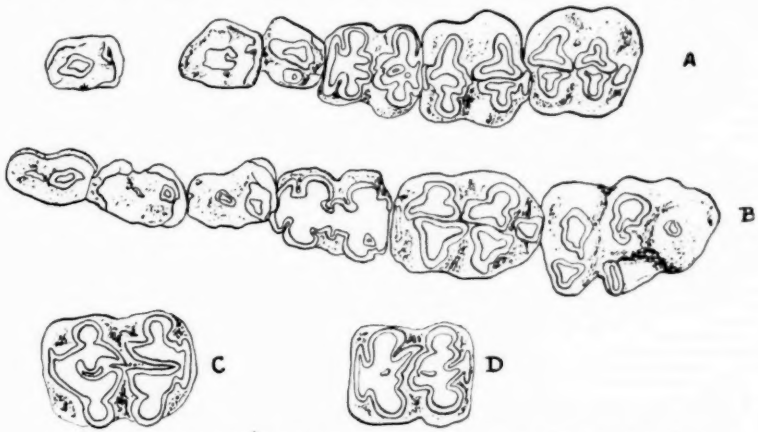


FIG. 1.—*Above*: Upper cheek teeth (A) and lower series (B) of an individual of *Hippopotamus amphibius* Linnaeus. *Below*: Two common variants from the symmetrical enamel pattern. (C) Lower second molar. (D) Upper first molar. One-third natural size. (Original.)

so that the more worn teeth have a squarer appearance than the younger ones. Upper teeth are slightly squarer than lowers at all but the earliest stages of wear.

The variations in pattern amongst individuals is amazingly large and little reliance can be placed upon variations in the symmetry of the columns or their secondary lobes. As a rule, however, the arrangement is a very symmetrical one. Typical upper and lower dentitions of an individual are shown in fig. 1, together with some variants of the normal pattern in individual teeth. It may also be noted that the last milk molars of the living hippopotamus, apart from their slightly smaller size, resemble closely the first or second molars of the adult.

The range of size variation appears to be fairly large. The following may be regarded as more or less normal dimensions of the molar teeth in an adult whose third molar is slightly abraded. Upper and lower teeth differ very little except that lower third molars are longer than uppers.

	M^1.	M^2.	M^3.	M_3.
Greatest length:	45–50 mm.	50–60 mm.	55–70 mm.	60–75 mm.
Greatest breadth:	40–50 mm.	45–55 mm.	45–60 mm.	
Breadth on grinding surface:	30–40 mm.	30–45 mm.	(30–40 mm.)	
Height of crown:	35–50 mm.	35–50 mm.	40–55 mm.	

The limiting sizes are not likely to exceed or fall below these figures by more than 5 mm. in breadth and 10 mm. in length, and even such specimens must be rare.

The fossil species and sub-species so far erected all lie within the range of variation of the living species, though they may be somewhat unusual variants. Fraas' *H. amphibius* var. *robustus* (1907) is not even near the upper limit of size, and Scott's *H. ponderosus* (1907) is within the known range of variation in form although narrower in proportion to its length than is usual in purely South African material. *H. amphibius* var. *venteri* is well within the normal range. *H. westphali* with its estimated third molar length of 82 mm. is exceptionally large, as also is *H. helmei*, but neither falls outside the limiting range of the living species. The "interlocking" of cusps and the high heel which Lyle regards as so important in these two species are seen, though not commonly, in living individuals. There may be some reason for separating *H. westphali* as a distinct species and including *H. helmei* and possibly even *H. ponderosus* with it, but until very much more material is available the justification for this procedure appears insufficient.

Family SUIDAE.

There have been described at various times since 1925 a moderately large number of supposedly extinct species of fossil pig, mainly of the wart-hog group. Until recently the comparative basis for the establishment of these species has been very uncertain and the position confused. A careful study by Shaw (1938) of the growth changes and variations in third molars of *Phacochoerus* has, however, now provided the essential background and made it unnecessary for such a study to be given here. Shaw effected a somewhat drastic revision of the fossil species which, however, is not accepted in its entirety and has been partially modified by Wells and the present writer (Wells and Cooke, 1942; Cooke and Wells, 1945) in the light of more recent discoveries, but these conclusions do not affect the status of Shaw's valuable study of the living wart-hog and are not matters of fundamental difference of opinion. Unfortunately the living South African bush pig, *Potamochoerus*, and the Central African *Hylochoerus* have not been similarly studied and their variations are more uncertainly known.

Genus POTAMOCHOERUS Gray, 1852.

Genotype: *Choiropotamus pictus* Gray (=*Sus porcus* Linn.).

Note.—The generic name *Choiropotamus* proposed by Gray in 1843 is preoccupied by a genus of extinct ungulate from France.

Potamochoerus koiropotamus * (Desmoulins).

Sus koiropotamus Desmoulins, 1831: Dictionnaire Classique d'Hist. Nat., 17, p. 139, pl. 10, fig. 2.

The skull is long and relatively narrow with a flattened inter-orbital region and a narrow parietal. The greatest length of the skull averages about 35–40 cm. and the breadth about 15–20 cm. The length of the row of cheek teeth is about 11–12 cm. The skull of the female has a narrow ridge running longitudinally backwards from the root of the canine, and in the male this forms a stout process of the maxillary bone. Three pairs of incisors are present in both jaws throughout life (unlike the wart-hog). The central pair in the upper jaw are thick and convergent, flanked by much smaller teeth more laterally placed, and the third incisors are small and peg-like. The two central pairs of lower incisors are moderately large and forwardly directed, the third incisors being rather smaller and placed close to the root of the canines. In the upper jaw there is a gap of 2–3 cm. between the third incisor and the root of the greatly enlarged upper canine. The upper canines curve round and are directed outwards and upwards, attaining an average length of 7–9 cm. The lower canines, or tuches, are almost triangular in cross-section and curve slightly upwards and outwards. They attain a length of 5–6 cm., but may grow to two or three times that length. The canines are larger in the male than in the female.

The cheek teeth of both jaws are rather similar, the upper teeth being somewhat wider than the lowers, but the first premolar is very small or absent in the lower jaw.

Average dimensions are:—

Upper Teeth:	P^1	P^2	P^3	P^4	M^1	M^2	M^3
Length:	10	11	13	14	15	21	32 mm.
Breadth:	5	7	11	14	16	20	20 mm.
Lower Teeth:	P_2	P_3	P_4	M_1	M_2	M_3	
Length:	8	13	15	15	19	35 mm.	
Breadth:	5	8	11	12	17	18 mm.	

In the upper teeth the first premolar is a simple, two-rooted conical tooth which may be separated from the broader, conical second premolar

* Allen, in his "Checklist of African Mammals," vol. lxxxiii, Bull. Harvard Mus. Comp. Zool., 1939, regards this as a sub-species of *P. porcus* Linn.

by a small diastema. The third premolar has four roots and presents a strong primary cone with a secondary one behind it. The fourth premolar has three primary cusps and the first molar four cusps. The first molar is abraded at a relatively early stage and usually presents a uniform tract of dentine in a normal dentition. The second molar has four primary cusps with a secondary posterior ridge and an anterior lobe, resembling in many cases the corresponding tooth of the hippopotamus. The third molar is a complex tooth with two pairs of primary cusps near the front and centre of the tooth respectively and a median posterior cusp, but several secondary cusps are interposed and the crown is multi-tuberculate in aspect and rather variable in different individuals.

The lower teeth are essentially similar, but in the absence or reduction of the first premolar, the second, third, and fourth premolars resemble more closely the upper first, second, and third premolars respectively. The third molar is longer than the upper one and the posterior cusps rather better developed. In wear both upper and lower teeth maintain their "cusped" character and show enamel margins to dentine areas, but never exhibit the ringed "columnar" structure of the wart-hog.

Typical upper and lower dentitions are shown in fig. 2.

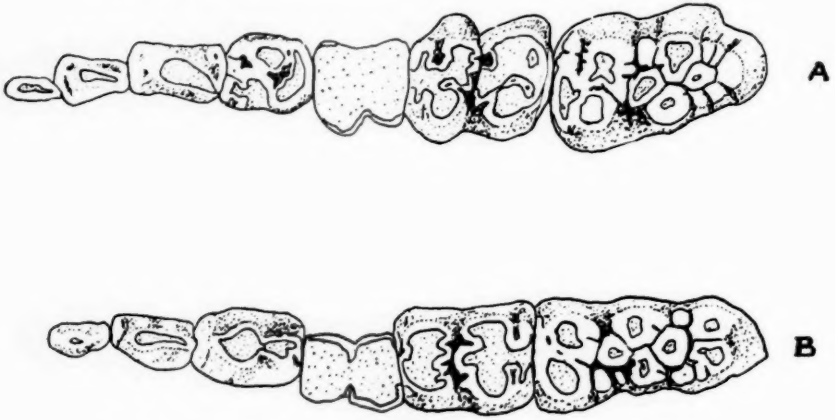


FIG. 2.—Upper cheek teeth (A) and lower series (B) of an adult individual of *Potamochoerus koiropotamus* (Desmoulins). Natural size. (Original.)

The bush pig is not widely known in fossil form, though teeth have been found in association with Later Stone Age implements and in superficial deposits. No extinct pigs of the *Potamochoerus* type are so far known in South Africa.

Genus PHACOCHOERUS Cuvier.

Genotype: *Sus aethiopicus* Gmelin (=*Aper aethiopicus Pallas*).

Note.—The generic name *Phacochoerus* Cuvier (1817) is really preceded by *Aper* Pallas (1766), but as this is merely the masculine of *Sus* it is best abandoned.

Two species of wart-hog have been recognised, namely *P. aethiopicus* and *P. africanus*, though the nomenclature of these two species has been much confused by the misuse of a large number of sub-specific names. *P. aethiopicus* is generally regarded as having become extinct, though Allen (1939) uses this as the only specific name and applies "*africanus*" to it as a sub-specific term. It would, however, appear certain that the Cape wart-hog of Pallas is now extinct and the living form should preferably be called *P. africanus*.

Lönnberg (1908) has attempted to give mensural criteria for the distinction of the different races, but Shaw (1938) has shown that the range of variation in Lönnberg's ratios is easily covered in a collection which would hardly include more than a single race. Owen (1845) stated that "in the Wart Hog of South Africa there are no incisive teeth in the upper jaw of the mature animal," whereas these are normally present in *P. africanus*. The evidence in support of this conclusion is, however, rather slender and it can hardly be regarded as a distinctive character. Van Hoepen (1932) has shown that a real difference exists in the development of the third molars of the two species, and his conclusions are confirmed by Shaw. It is accordingly only in this feature that the two species can be distinguished with certainty and then only at certain stages of growth, so that the general description of the skull and teeth of *P. africanus* which follows may be taken to apply equally to *P. aethiopicus*, as far as is known, with the exception of the development of the third molar.

Phacochoerus africanus (Gmelin).

Sus africanus Gmelin, 1788; Linnaeus, Syst. Nat., ed. 13, 1, p. 220.
Phacochoerus aeliani of many authors.
Phacochoerus stenobunus Pia, 1930; Centr. Min. Geol. Pal., Abt. B., No. 2, pp. 76–83, figs. 1–2.
Phacochoerus africanus, Van Hoepen and Van Hoepen, 1932: Idem., pp. 50–51, figs. 37–40.

The skull of *Phacochoerus* differs considerably from that of *Potamochoerus* in presenting a broader aspect with thickened zygomatic arches and enlarged bony bosses formed round the sockets of the upper canines.

The skull is wide and concave between the orbits, whereas in the bush pig this area is flattened or even convex. In dimensions the skull does not differ greatly from *Potamochoerus*, the normal length being 35–40 cm., breadth 20–25 cm., while the cheek teeth occupy only about 8 cm.

The normal number of incisor teeth comprises a single pair in the upper jaw and two or three pairs in the lower jaw. The pair of third lower incisors never develops in some animals (Shaw, 1939), while there is a tendency for the shedding of the upper incisors and even the other incisors in old animals. A similar reduction affects the cheek teeth, so that in some very old animals only the canines and third molars remain. The two upper incisors are short and thick and are directed towards each other. The lower incisors comprise two pairs of strong but moderately small cylindrical teeth forwardly directed and obliquely abraded. If they are present the outer pair of lower incisors is small and peg-like.

The upper canines are long and curve outwards, upwards, and backwards, frequently attaining a length of 25 cm., and they are rhomboidal or tetragonal in section. The lower canines are more or less triangular in section and are curved outwards and upwards, preserving a sharp edge by attrition with the upper tusks. They are not as long as the uppers and average about 10–15 cm.

The complete series of cheek teeth appears to comprise a maximum of five or six upper or lower teeth on each side, but there are rarely more than four teeth in each jaw of any specimen, and in mature animals this is soon reduced to two. In old animals the third molar lies alone in each jaw. The true first premolar does not seem to form in *Phacochoerus*, and the second premolar is also frequently suppressed in both jaws. In the upper jaw the third premolar is a small tooth about 5 mm. broad and 6 mm. long with two cusps. The fourth premolar has four cusps and is almost square with a side of 8–9 mm. In wear the lateral pairs of cusps fuse first and then unite anteriorly. The first molar, which is erupted at an early stage of growth, is rarely seen except as a stump of dentine, but in very young specimens this tooth shows six cusps arranged in two triangles of three each, and the posterior trefoil retains its identity until wear is quite well advanced. The first molar is shed early, and the gap becomes closed by the advance of the second molar into contact with the fourth premolar. The little worn first molar measures 12–14 mm. in length and 10–13 mm. in breadth. The second molar is a much more oblong tooth, measuring 12–14 mm. in breadth and 18–22 mm. in length on the average. Its pattern is complex and foreshadows the three-rowed arrangement of islets in the third molar, but is very variable and changeable in wear. Essentially there appear to be two pairs of lateral columns which unite to form an anterior crescentic enamel island. Several smaller columns lie in an irregular row between the lateral

pairs and unite with them and with each other to form irregular enamel islands. Two small columns form the back of the tooth in early wear and unite as attrition proceeds. The height of the unworn crown above the dentine base is not usually more than 1 cm. The third molar is a very much larger tooth with columns of a height often exceeding 4–5 cm., and its structure will be described in more detail below. The upper dentition of a young wart-hog is shown in fig. 3.

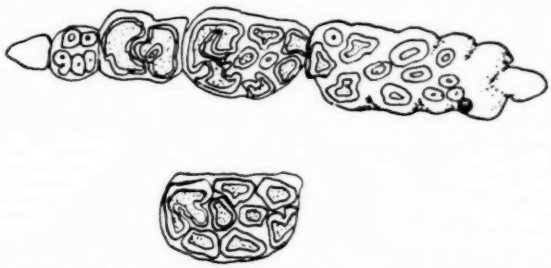


FIG. 3.—*Phacochoerus africanus* (Gmelin). *Above*: Upper cheek teeth of a young individual to show the form and patterns of the early teeth. *Below*: Enamel pattern of lower second molar of the same individual. Natural size. (Original.)

In the lower jaw the third premolar is a simple tooth with two cusps, and the fourth premolar has a somewhat triangular form made up of a large anterior cusp and two smaller posterior ones. The length of this latter tooth is only about 10 mm. and its greatest breadth 7–8 mm. on the average. The first and second molars have essentially the same structure as the corresponding upper teeth, but are narrower by about 1–2 mm. A lower second molar is shown in fig. 3. The third molar also resembles closely the corresponding upper tooth, and it is the third molar which is the most characteristic of the species.

The third molars develop from semi-persistent pulps and root formation takes place just before, or at about the same time as, the eruption of the hindmost columns is completed, but before these columns commence to be abraded. Structurally each tooth consists of two lateral rows of columns (usually six to seven on each side) with a central row of smaller columns (usually eight to eleven). The lateral columns tend to be sub-triangular in section or to be transversely flattened and antero-posteriorly elongate, while the median columns are rounder. The height of the columns is about 4–5 cm.

Shaw (1939) has given an excellent account of the changes in form consequent upon growth and attrition which cannot be repeated here, though the remarks which follow are largely based on Shaw's work.

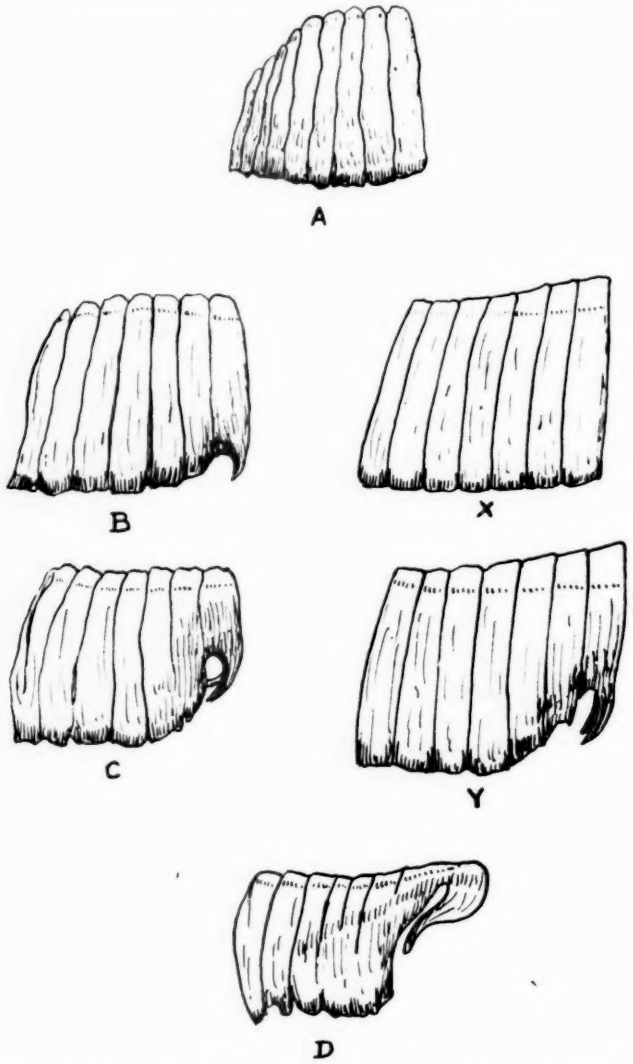


FIG. 4.—Changes in shape and root formation in third molars of *Phacochoerus africanus* (Gmelin) and *P. aethiopicus* (Pallas). A. Early form of the young tooth in either species. B. Roots formed on anterior columns in *P. africanus* but posterior columns unworn. C. Roots well formed and hindmost column just in wear (*P. africanus*). X. Columns all in wear but roots not yet formed (*P. aethiopicus*). Y. Anterior roots moderately well formed and posterior column well worn (*P. aethiopicus*). D. Well-worn third molar of old individual of either species. Three-fifths natural size. (Original partly after Shaw.)

In the early stages of growth each column has approximately the same diameter at its occlusal and basal ends, but a gradual downward expansion occurs, giving each column a slightly conical form, and later adjoining

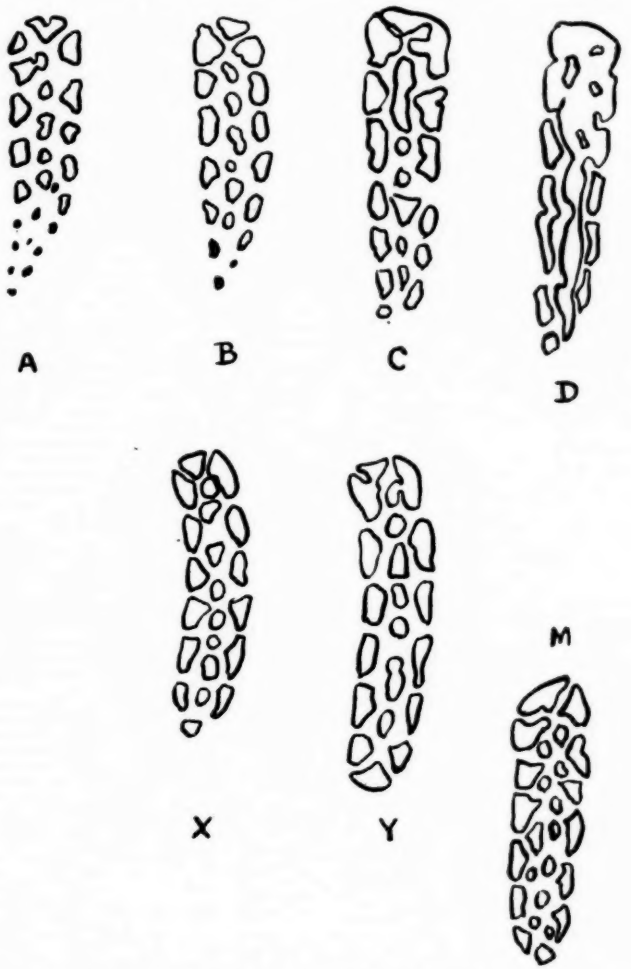


FIG. 5.—A–D, X, Y: Enamel patterns of teeth at the stages corresponding to Fig. 4. Lower Right (M): Enamel pattern of third molar of *Phacochoerus africanus* showing the abnormal state with two rows of median columns. Natural size. (Original.)

columns unite to give a smaller number of more complex columns. As attrition proceeds a wider part of each column is exposed and the individual enamel islands increase in size and later fuse with one another to produce complicated patterns. The three foremost islands unite at an early stage and form a complex anterior island which Van Hoepen (1932) has termed the "anterior complex." With advanced wear a very complicated pattern results, and this bears little resemblance to the symmetrical pattern of the young tooth. A few growth stages are illustrated in fig. 4 and the corresponding enamel patterns appear in fig. 5.

Shaw has shown that in some specimens there are four rows of columns instead of the usual three, but this condition is a rare one. It does, however, add greatly to the complexity of the enamel pattern in such teeth. An example is illustrated in fig. 5.

According to Shaw: "In lower molars the average number of columns is seven buccal, seven lingual and eight median, but the marginals vary from six to nine and the medians from seven to thirteen. In upper molars seven is the average number of columns in each of the three series, but the marginals vary from six to ten and the medians from seven to thirteen. In the majority of cases the columns on the buccal and lingual sides are of equal number, but in some cases more columns are present on one side than on the other. Supernumerary columns are occasionally present.

"At first sight these (upper and lower) teeth appear identical, but close investigation discloses a number of differences. For example the uppers are normally wider labio-lingually than the lowers. . . . It is proposed to refer only to those differences which assist in identifying loose upper and third molars. Van Hoepen (1932) pointed out one method of doing this. He showed that in an upper molar 'the second left or right * side cone protrudes further from the tooth than any of the other side cones,' while in a lower molar no one cone protrudes further outwards than the others. In the writer's experience this method is extremely satisfactory, but in some cases the degree of protrusion of the second cone is very slight and thus not easily recognisable.

"The presence of four marginal columns and the absence of median columns at the anterior portion will in all cases identify an upper third molar. Alternatively, the presence of only one median column at the anterior extremity will identify a lower third molar."

Shaw does not give average and extreme limits of size of third molars of *P. africanus*, but the following appears to the present writer to be a representative average for a tooth fully erupted but at an early stage of root formation (*e.g.* B, C, in fig. 4).

* Actually the inner side. (H. B. S. C.)

	M_3.	M^3.
Greatest length:	50–60 mm.	55–65 mm.
Length of occlusal surface:	45–50 mm.	45–55 mm.
Greatest height:	45–55 mm.	50–65 mm.
Breadth of occlusal surface:	11–14 mm.	12–15 mm.

Specimens as much as five mm. in excess of the limits of length and height given above are extremely rare and the majority of living specimens lie closer to the lower than to the upper limits of these dimensions.

A pair of typical upper and lower teeth is shown in fig. 6.

Fossilised or semi-fossilised teeth which cannot be distinguished from the living form have been found in superficial deposits in various parts of the country, but are rarer than those of the extinct *P. aethiopicus*. Larger teeth of the "africanus" type are found but appear to be specifically distinct.

Phacochoerus aethiopicus (Pallas).

Aper aethiopicus Pallas, 1767: Spicilegia Zool., pt. 2, p. 2, pl. 1.
Phacochoerus venteri Dreyer and Lyle, 1931: "New Fossil Mammals and Man," p. 11, pl. 1 (8).
Phacochoerus meiringi Dreyer and Lyle, 1931: Idem., p. 12, pl. 1 (6).
Phacochoerus dreyeri Dreyer and Lyle, 1931: Idem., p. 12, pl. 1 (7).
Phacochoerus aethiopicus, Van Hoepen and Van Hoepen, 1932: Pal. Nav. Nas. Mus. Bloemfontein, iv, pp. 49–50, figs. 31–36.

The recently extinct South African wart-hog appears to have resembled the living *P. africanus* to a very high degree, and until 1932 the only skull differences between the two species were supposed to be the early shedding of the upper incisors and the metrical criteria of Lönnberg (1908). Shaw (1938) has shown that these criteria rest upon very uncertain foundations. Van Hoepen (1932) found for the first time that in *P. aethiopicus* root development was delayed in the third molars until well after all the columns had reached the grinding surface and were in wear. This conclusion has been confirmed by Shaw (1939) who states that this condition is not found in third molars of *P. africanus*. As far as can be learned, however, there is no other significant structural difference between the two species, and it is thus only in teeth between certain limits of development that the third molars of the two species may be distinguished with certainty. This is shown in fig. 6, illustrating the fact that before all the columns are developed the two species present the same appearance and that the same is again true in advanced wear. In the long intermediate stage, however, two types can be recognised: (1) Teeth with posterior columns not yet at the grinding surface but with anterior roots developing or developed (A and B). (2) Teeth with even their hindmost columns in wear and yet lacking any roots

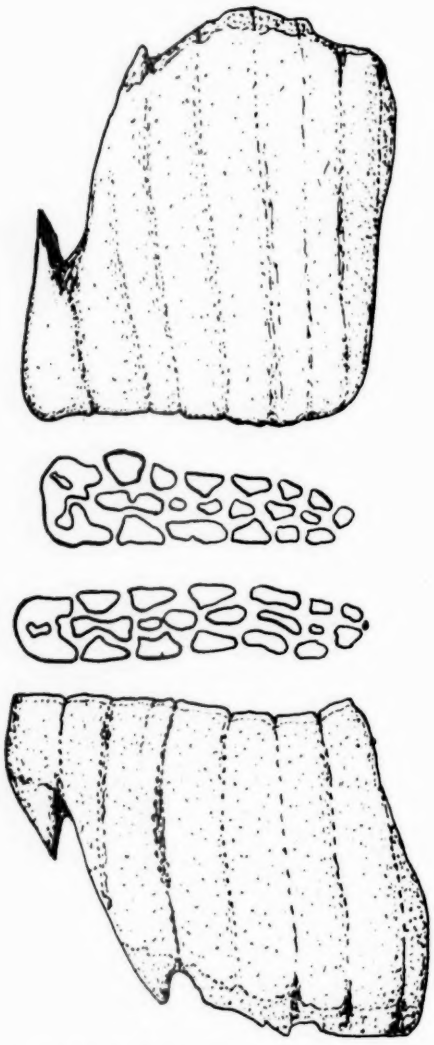


FIG. 6.—Lateral and occlusal views of typical upper and lower third molars of *Phacochoerus africanus* (Gmelin). Natural size. (Original.)

(X) or having incipient or small roots on the anterior columns, but with the posterior columns well worn (Y). The first category is the "*africanus*" type and the second the "*aethiopicus*" type.

Van Hoepen (1932) suggested that differences in the structure of the columns was evident, but this does not seem to be confirmed. He stated that in *P. aethiopicus* the sides of the columns are parallel and do not broaden out at their bases as they do in the living species. Shaw states that his "material fails to confirm this view, but it is found that broadening of the bases of the columns occurs at a later stage in *P. aethiopicus* than in *P. africanus*. The investigation showed in fact that the third molars of *P. aethiopicus* and *P. africanus* have the same characters, but whereas in the latter species certain characters develop early, in *P. aethiopicus* these characters fail to develop until late in life."

The average dimensions of *P. aethiopicus* teeth appear to cover approximately the same range as those of *P. africanus*. A pair of typical upper and lower teeth is shown in fig. 7.

The three species *P. venteri*, *P. meiringi*, and *P. dreyeri* proposed by Dreyer and Lyle (1931) have been referred by Van Hoepen (1932) to *P. aethiopicus* or, in the case of the last named, to *P. africanus*. *P. dreyeri* is however, rootless and fully erupted, so that it appears more likely to be *P. aethiopicus*, and there seems little doubt that all three species are synonyms of that form.

Shaw (1939) referred all Dreyer and Lyle's and all Van Hoepen's Phacochoere-like species and genera to *P. africanus* or *P. aethiopicus*, but in view of later discoveries Wells and the writer (1942–1945) have modified this conclusion and recognise two other species—*P. helmei* Dreyer and Lyle, and *P. compactus* Van Hoepen and Van Hoepen—in addition to the giant *P. altidens* Shaw and Cooke.

Phacochoerus helmei Dreyer and Lyle.

Phacochoerus helmei Dreyer and Lyle, 1931: "New Fossil Mammals and Man," pp. 9–11, pl. 1 (3, 4, and 5).

Phacochoerus africanus, Van Hoepen and Van Hoepen, 1932: Pal. Nav. Nas. Mus. Bloemfontein, ii, p. 48.

Phacochoerus laticolumnatus Van Hoepen and Van Hoepen, 1932: Idem., pp. 51–53, figs. 41–45.

Phacochoerus aethiopicus, Shaw, 1939: Trans. Roy. Soc. S. Afr., xxvii, pp. 78–80.

Phacochoerus helmei, Wells and Cooke, 1942: Trans. Roy. Soc. S. Afr., xxix, pp. 224–226, fig. 10.

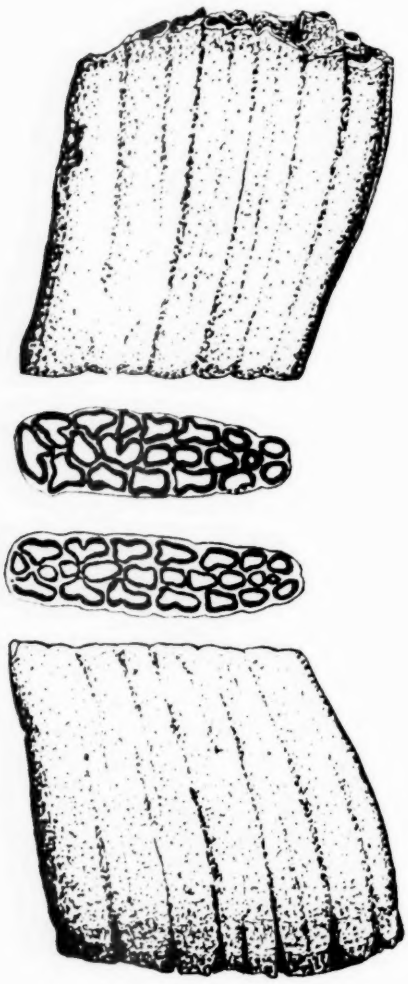


FIG. 7.—Lateral and occlusal views of typical upper and lower third molars of *Phacochoerus aethiopicus* (Pallas). Natural size. (From Wells and Cooke.)

Type: Upper and lower third molars of the left side, fig. 8.
Locality: Floris Bad.
Horizon: Deposits of thermal spring.
Dimensions:

	M^3.	M_3.
Occlusal length:	63·5 mm.	61 mm.
Occlusal breadth:	12·5 mm.	12 mm.
Height not given.		

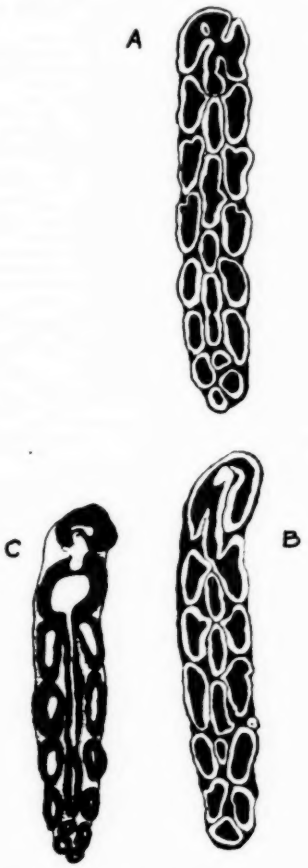


FIG. 8.—Enamel patterns of type left lower and upper molars of *Phacochoerus helmei*, Dreyer and Lyle. A. Occlusal surface of lower third molar. B. Occlusal surface of upper third molar. C. Enamel pattern of upper third molar seen from below. Natural size. (From Dreyer and Lyle.)

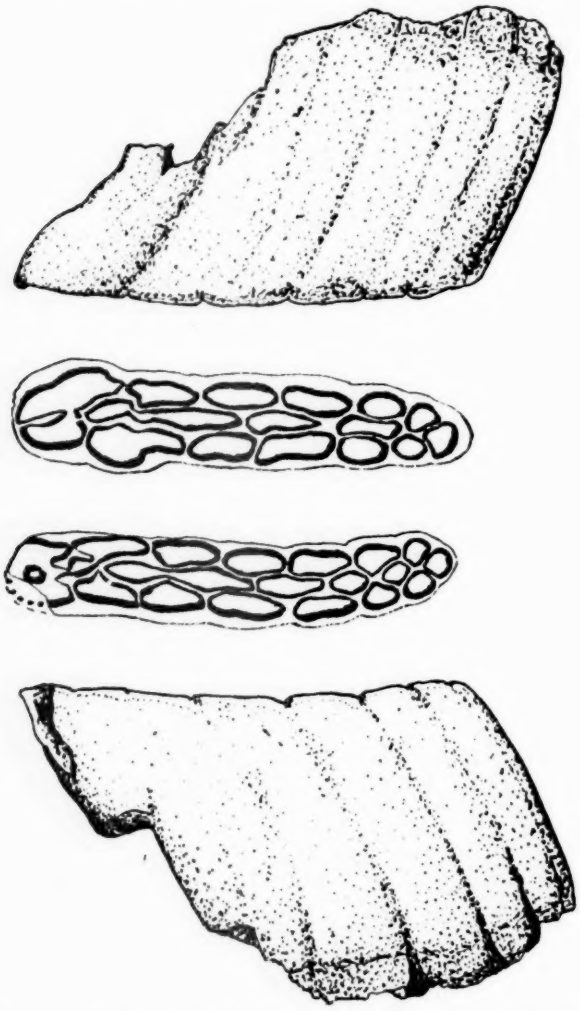


FIG. 9.—Lateral and occlusal views of upper and lower third molars referred to *Phacochoerus helmei* Dreyer and Lyle, from Vlakkraal. Natural size. (From Wells and Cooke.)

Neotypes: Upper and lower third molars of the right side. Fig. 9. S.A. Mus., No. 10937.

Locality: Vlakkraal (near Floris Bad).
Horizon: Thermal spring deposits.

Dimensions:	M^3.	M_3.
Maximum length:	69·0 mm.	69·0 mm.
Maximum height:	44·0 mm.	46·0 mm.
Occlusal length:	68·5 mm.	68·0 mm.
Occlusal breadth:	16·0 mm. (anterior)	13·5 mm.
	14·0 mm. (median)	

This species develops roots in the "*africanus*" manner, but root formation may occur slightly later than in typical *P. africanus*. This is shown by the abrasion pattern reaching a slightly more advanced stage than that found in *P. africanus* at a corresponding stage of root formation. In size it lies at or close to the extreme upper limit of variation of *P. africanus*. The distinction from the living species appears necessary on account of the consistent occurrences in the fossil state of teeth of comparable dimensions and the very great rarity of such large teeth in the living species. Furthermore, the columns are consistently more elongated than in the living form and the roots appear to form at a slightly later stage, bringing this species a little closer to *P. aethiopicus*.

These characters are also found in the species described by Van Hoepen as *P. laticolumnatus*, and it is probable that this is a synonym of *P. helmei*. The dimensions of the Van Hoepen's type specimen are:—

	M^3 (Nas. Mus., No. C. 34).
Height (anterior):	58 mm.
Height (posterior):	37 mm.
Occlusal length:	72 mm.

Two referred teeth from Vlakkraal (Wells and Cooke, 1942) have the following dimensions:—

	M^3.	M_3.
Maximum length:	69·0 mm.	61·0 mm.
Maximum height:	47·0 mm.	52·0 mm.
Occlusal length:	67·5 mm.	56·5 mm.
Occlusal breadth:	13·5 mm.	13·5 mm.

Phacochoerus compactus (Van Hoepen and Van Hoepen).

Stylochoerus compactus Van Hoepen and Van Hoepen, 1932: Pal. Nav. Nas. Mus. Bloemfontein, ii, pp. 53–56, figs. 46–47.

Synaptochoerus hieroglyphicus Van Hoepen and Van Hoepen, 1932: Idem., pp. 56–57, figs. 58–64.

Phacochoerus aethiopicus ? Shaw, 1939: Trans. Roy. Soc. S. Afr., xxvii, pp. 80–82.

Phacochoerus compactus, Wells and Cooke, 1942: Trans. Roy. Soc. S. Afr., xxix, pp. 221–223, fig. 9.

Phacochoerus compactus, Cooke and Wells, 1945: S. Afr., J. Sci., xlii.

Type: Upper third molar of the right side. Nas. Mus., No. C. 801 (fig. 10).

Locality: ?.

Dimensions:

	RM^3.
Height:	76 mm.
Occlusal length:	49 mm.
Occlusal breadth:	15 mm.

Third molars of this species belong to the "*aethiopicus*" type as far as root formation is concerned, but are distinguished from *P. aethiopicus* by their greater size and complexity of columnar structure. The teeth lie in dimensions at or above the upper limit of size of the recent species and are notably taller and wider. The columns are more elongated and have a more irregular outline than in *P. aethiopicus*. The marginals tend to have strongly developed inwardly projecting lobes which, in the anterior part of the tooth, meet in the mid-line, interrupting the series of median columns and tending to become united with the median columns to produce complex figures. A further indication of the complexity of the tooth structure is to be found in the frequent occurrence of more than one row of median columns and in the development of numerous small accessory conules ("paramolars") at various levels. Such "paramolars" do occur in the living species but are rare.

Shaw has advanced what appears to be entirely adequate evidence that the characters upon which the genus *Stylochoerus* was established by the Van Hoepens are not truly of differential value, since they are found sporadically in the recent species. The type tooth of the species *compactus*, however, is considerably larger than the corresponding normal recent tooth, and appears to lie outside the reasonable range of variation of *P. aethiopicus*. It is considered, therefore, that *compactus* may, with good reason, be regarded as a valid species of the genus *Phacochoerus*, related to *P. aethiopicus* by its lack of early differentiated roots, but distinguished by its greater size and a tendency towards the development of a more complex enamel pattern. Shaw has shown that the presence of more than three rows of columns is an occasional feature of the living forms, and is therefore not of specific importance. However, in teeth as large as those of *P. compactus* the development of an extra row of columns may well be a more common feature, while small accessory conules on the side of the teeth indicate the same tendency. In both its size and its enamel characters, *P. compactus* lies largely in an intermediate position between *P. aethiopicus* and the gigantic *P. altidens* Shaw and Cooke.

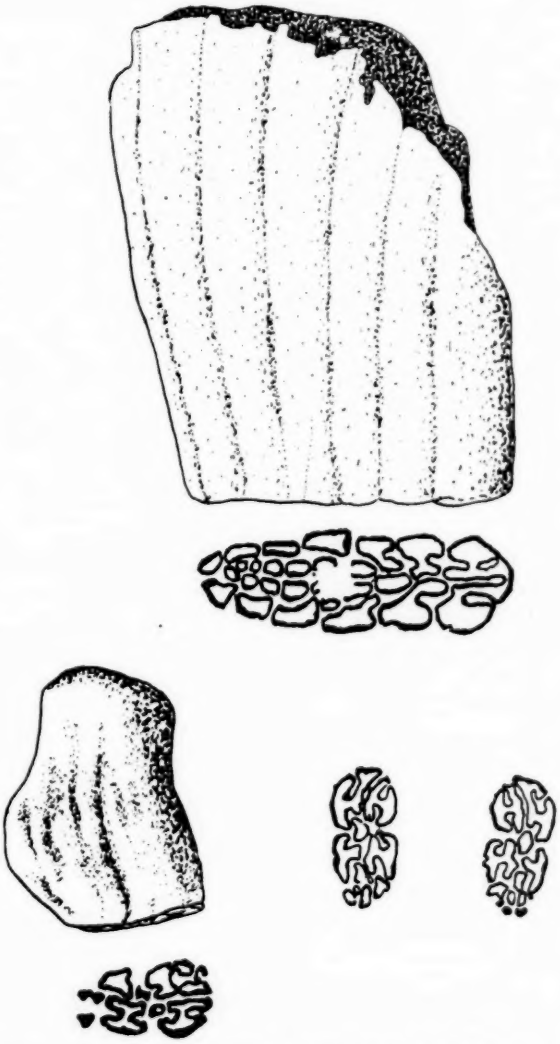


FIG. 10.—*Phacochoerus compactus* (Van Hoepen and Van Hoepen). *Above*: Occlusal and lateral views of the type upper right third molar. *Lower left*: Occlusal and lateral views of probable upper right second molar. *Lower right*: Enamel patterns of probable left and right first molars. Natural size. (Redrawn from Van Hoepen and Van Hoepen.)

The type tooth is shown in fig. 10, and a referred example from Vlakkraal (Wells, Cooke and Malan, 1942), cited as a neotype, has previously been figured illustrating the characters described. The dimensions of this referred tooth (Dept. Anat., 896/4 C) are given below together with three other teeth from the same locality now in the South African Museum (10937 and two numbered 10939).

	RM^3, 896/4C.	LM^3, 10937.	M^3, 10939.	M^3, 10939.
Maximum height:	62·0 mm.	62·0 mm.	52+ mm.	56+ mm.
Maximum length:	59·0 mm.	57·5 mm.	54+ mm.	49+ (? 56) mm.
Occlusal length:	52·5 mm.	51+ mm.	50 mm.	45+(52) mm.
Occlusal breadth:	15·5 mm.	15·5 mm.	15·5 mm.	16 mm.

The Van Hoepens have referred to this species two second molars of the left side and right side respectively, and also a left and a right first molar. The dimensions of these teeth are given as:—

	RM^2.	LM^1.
Height:	40 mm.	18 mm. (without roots).
Greatest length:	30 mm.	25 mm.
Occlusal breadth:	12 mm.	11 mm.
Greatest breadth:	16·5 mm.	

All these teeth are a good deal larger than those of the living species and their columnar structure is more complex, showing the same elongate tendency as is exhibited in the third molars of *P. compactus* and *P. altidens* (below). No evidence of their association with the type of *P. compactus* is advanced by the Van Hoepens, but they are more or less what should be expected for the corresponding teeth of that species and may conveniently be referred to it. These teeth are figured with the type third molar (fig. 10).

The Van Hoepens (1932) described from the same locality as "*Stylochoerus*" *compactus* large lower teeth which they called *Synaptochoerus hieroglyphicus*. Whereas the teeth referred to "S" *compactus* are uppers, those of "*S*" *hieroglyphicus* are lowers. The characters of these lowers are just what might be expected for the lowers of "*S.*" *compactus*. In view of this fact and their known association, it seems highly probable that they belong to the single species *Phacochoerus compactus*. Fig. 11 shows the lower teeth described by the Van Hoepens.

Phacochoerus altidens Shaw and Cooke.

Phacochoerus altidens Shaw and Cooke, 1941: Trans. Roy. Soc. S. Afr., xxviii, pp. 296–297, pl. liv (3 and 4).

Type: ? Lower third molar broken anteriorly. Arch. Sur., No. 31 (fig. 12).

Locality: Larsen's Pits, Riverview Estates, opposite Windsorton, C.P.
Horizon: Probably middle phase of Younger Gravels of Vaal River.

Dimensions:	(As preserved)	(Estimated.)
Maximum height:	81 mm.	86 mm.
Greatest length:	64 mm.	75 mm.
Occlusal length:	41 mm.	73 mm.
Greatest occlusal width:	18·5 mm.	19–19·5 mm.

FIG. 11.—*Phacochoerus compactus* (Van Hoepen and Van Hoepen). *Above*: Enamel pattern and lateral views of anteriorly incomplete referred right lower third molar. *Below*: Occlusal view of referred lower left third molar, formerly the type of *Synaptochoerus hieroglyphicus* Van Hoepen and Van Hoepen. Natural size. (Redrawn after Van Hoepen and Van Hoepen.)

This giant phacochoere probably exceeded in size the average fully developed *P. africanus* or *P. aethiopicus* third molars by about two-thirds in each dimension. It is also very considerably larger than *P. compactus* which, in fact, lies both in size and in characters about midway between this species and *P. aethiopicus*. All the columns are antero-posteriorly

elongate and there are two rows of elongate median columns with evidence of the occasional development of additional median columns. Accessory "paramolars" are present and appear to develop near the junction between

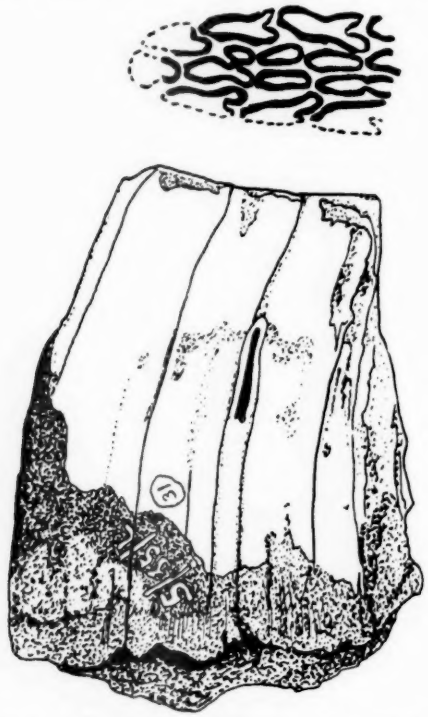


FIG. 12.—Occlusal and lateral views of type third molar of *Phacochoerus altidens* Shaw and Cooke. Natural size. (Original.)

the lateral columns. It is not possible to determine whether the species belongs to the "*africanus*" or the "*aethiopicus*" group as far as root formation is concerned, but it appears likely that it is of the "*aethiopicus*" type.

No specimens other than the type are certainly known, but several small fragments from the Vaal River gravels resemble the type and probably belong to the same species.

Genus NOTOCHOERUS Broom.

Genotype: *Notochoerus capensis* Broom.

Large pigs possessing third molars with moderately high to high columns

arranged much as in *Phacochoerus* but with root formation beginning much earlier and rather resembling the roots found in *Sus*. The anterior columns are infolded, but this complexity decreases posteriorly. The lateral columns are separate in the upper part but widen and unite only near their bases.

Notochoerus capensis Broom.

Notochoerus capensis Broom, 1925: Rec. Albany Mus., iii, pp. 308–309, figure.

(*non Notochoerus capensis* syn. *meadowsi* Shaw, 1938: Trans. Roy. Soc. S. Afr., xxvi, pp. 25–37, and Trans. Roy. Soc. S. Afr., xxvii, pp. 88–92.)

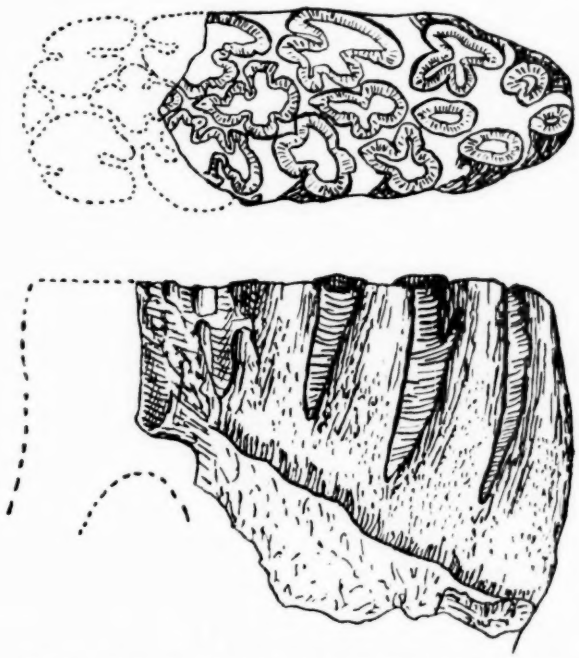


FIG. 13.—Occlusal and lateral views of type lower third molar of *Notochoerus capensis* Broom. Natural size. (From Broom.)

Type: Damaged lower third molar of the left side (fig. 13). P.E. Mus.
Locality: Longlands, near Kimberley, C.P.
Horizon: Diamond gravels of the Vaal River.

Dimensions:

Greatest length (as preserved): 64 mm. (79 mm. as restored).
Greatest width at second pair of columns: 30 mm.
Height of posterior column: 45 mm.

As restored by Broom the third molar of the type possesses "five pairs of lateral cusps and six median cusps, and the median cusps are so large that they separate the lateral cusps from each other as they also do in *Phacochoerus*. The anterior cusps are much infolded as in *Sus*, but the posterior are simple rounded pillars as in *Phacochoerus*."

The individual columns taper markedly upwards and are united only a little above the indistinct cingulum which separates them from the roots. Through almost the entire height of the crown (probably about 5 cm.) the lateral columns are quite distinct and well separated (fig. 13). The median columns are folded almost as much as the lateral so that the crown pattern is complex.

Shaw (1938) suggested that this species was identical with *N. meadowsi* Broom and later (1939) that Broom's restoration was incorrect and that only the foremost column of the anterior complex was lacking through injury. This restoration is not convincing and lessens rather than increases the resemblance of the two species.

Genus TAPINOCHOERUS Van Hoepen and Van Hoepen.

Genotype: *Tapinochoerus modestus* Van Hoepen and Van Hoepen.

Large pigs possessing third molars with high columns arranged in a pattern resembling *Notochoerus* or *Phacochoerus* but with root formation resembling *Phacochoerus africanus*. The lateral columns are contiguous for at least half their height above the indefinite cingulum.

Very possibly this may be regarded as only a sub-genus of *Phacochoerus*.

Tapinochoerus meadowsi (Broom).

Notochoerus meadowsi Broom, 1928: Ann. S. Afr. Mus., xxii, pp. 439–441, fig. 1.

Phacochoerus meadowsi, Dreyer and Lyle, 1931: "New Fossil Mammals and Man," pp. 9–11.

Tapinochoerus meadowsi, Van Hoepen and Van Hoepen, 1932: Pal. Nav. Nas. Mus. Bloemfontein, ii.

Kolpochoerus sinuosus Van Hoepen and Van Hoepen, 1932: Idem., pp. 59–61, figs. 72–77.

pars *Notochoerus capensis* syn. *meadowsi*, Shaw, 1938: Trans. Roy. Soc. S. Afr., xxvi, pp. 25–37, and Trans. Roy. Soc. S. Afr., xxvii, pp. 88–92.

Type: Lower third molar of the left side (fig. 15). M.M.K.
Locality: Kimberley District.
Horizon: Diamond gravels of the Vaal River.
Dimensions:

Greatest length (at base):	76 mm.
Greatest width (at base of columns):	19 mm.
Width across anterior pair of columns:	16 mm.
Greatest height (4th column):	64 mm.

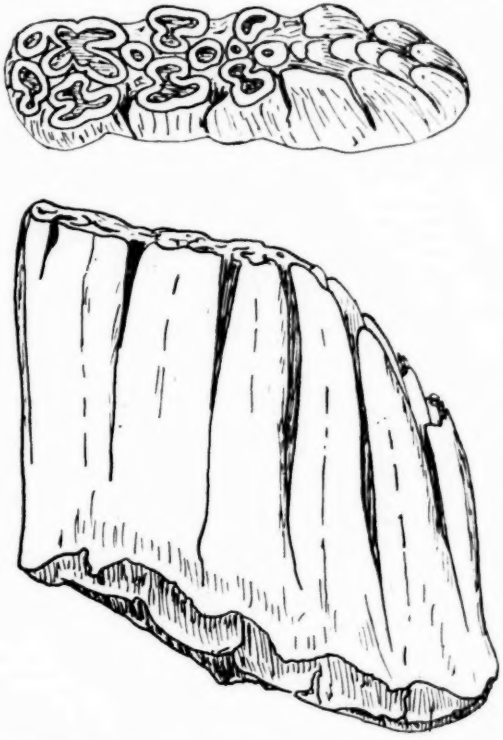


Fig. 14.—Occlusal and lateral views of type lower third molar of *Tapinochoerus meadowsi* (Broom). Natural size. (Redrawn from Broom.)

In the type description Broom states that "the tooth is made up of two rows of long pointed cusps with between them a median row of smaller cusps. The shape and arrangement of these cusps will be most readily understood from the figures given. As will be seen, the outer and inner cusps are six in number, and the anterior ones considerably convoluted and

the posterior much smaller and rounded. The median cusps are slender and rounded." It will also be noted, though Broom does not mention the fact,

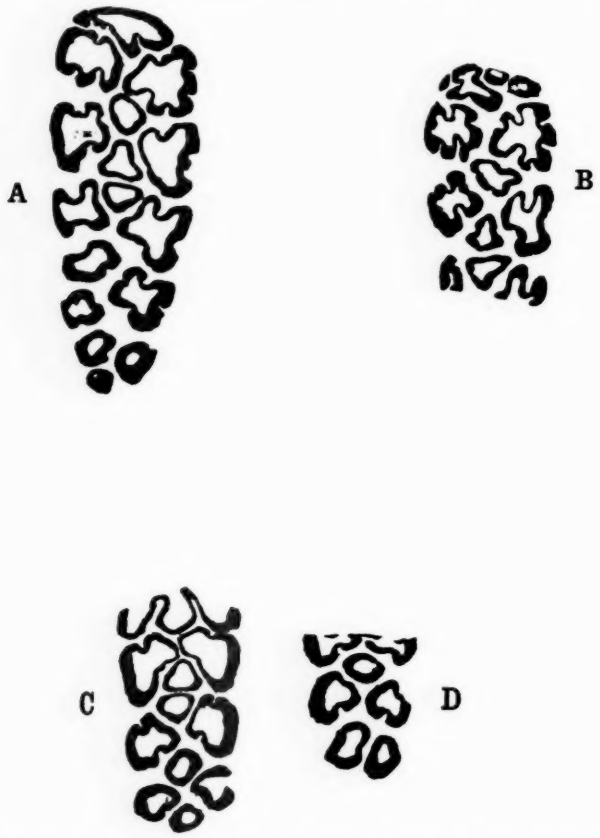


FIG. 15.—*Tapinochoerus meadowsi* (Broom). Enamel patterns of (A) left upper third molar, (B) right (?) upper third molar, (C and D) posterior portions of lower third molars referred by the Van Hoepens to *Kolpochoerus sinuosus* and by Shaw to *Notochoerus capensis*. All natural size. (From Van Hoepens.)

that the lateral columns lie closely together as in *Phacochoerus* and are actually in contact for the greater part of their height. Other specimens confirm this description and also show that only an indistinct cingulum demarcates the columns from their roots. The upper teeth differ from the lower in being wider and more complex in columnar structure with the

lateral columns a little more distinctly separated from each other but not nearly as distinct as in *Notochoerus capensis*.

The columns of *T. meadowsi* differ from those of *N. capensis* in their contiguity throughout their height, and their root formation is widely different. *N. capensis* has strong roots, whereas in *T. meadowsi* root formation resembles that of *Phacochoerus*. Indeed, it would seem that the differences between *N. capensis* and *T. meadowsi* are not merely of specific but, as both Dreyer and Lyle (1931) and the Van Hoepens (1932) have proposed, of generic rank. *N. capensis* lies closer to *Mesochoerus* and *T. meadowsi* closer to *Phacochoerus*. In fact Dreyer suggested that *T. meadowsi* be included in *Phacochoerus*. It appears, however, to lie more in a position intermediate between *Phacochoerus* and *Notochoerus*, and it is therefore proposed to revive the Van Hoepens genus *Tapinochoerus* for the reception of "*N.*" *meadowsi*.

Shaw (1938) gives the following dimensions for three teeth from the Sterkfontein Caves:—

	M_3(A).	M_3(B).	M^3(C).
Greatest length (at base):	79 mm.	77 mm.	62 + mm.
Greatest width (at base):	20 mm.	20 mm.	30 mm.
Greatest height (3rd cone):	68 mm.	66 mm.	60 mm. (estimated).

These three teeth Shaw believes to belong to the same individual. (A) shows seven pairs of lateral cones and twelve median cones; (B) has six pairs of laterals and eleven median cones, while (C) has six pairs of laterals and ten median cones as well as four "paramolars" or "extra" cones. A section through the centre of the upper tooth shows that the columns increase in size through lateral fusion, become more complex in form and decrease in number.

The Van Hoepens have described under the name *Kolpochoerus sinuosus* three teeth from Cornelia, Orange Free State, which have the following dimensions:—

	LM^3 (C. 798).	RM_3 (C. 799).	M_3 (C.800).
Occlusal length:	63 mm.	41 + mm.	41 + mm.
Greatest width:	25 mm.	21·5 mm.	20·5 mm.
Width posteriorly:		17·5 mm.	16·5 mm.
Crown height (anteriorly):	11 mm.	18·0 mm.	4·0 mm.
Crown height (posteriorly):	28 mm.	25·5 mm.	15·0 mm.

All these teeth are greatly worn. Their enamel patterns are shown in fig. 15. They agree moderately well with the teeth of *N. meadowsi*, but fail to show the extensive fusion of columns exhibited in Shaw's sectioned molar. They are considerably smaller than *N. capensis* as restored by Broom, and

differ also from Shaw's reconstruction in having the lateral columns more closely in contact. They also possess not less than five pairs of laterals compared with four in Shaw's reconstruction and five in Broom's, and cannot reasonably be identified with *N. capensis*.

Broom has recovered several *T. meadowsi* molars from the Sterkfontein Caves and the lowers are entirely consistent with the type and with Shaw's material. The only upper teeth so far recovered, however, agree in indicating the greater width of these teeth (25–30 mm.) as compared with the lowers (15–22 mm.), and appear also to be rather shorter antero-posteriorly (60–70 mm.) compared with the lowers (65–75 mm.). They thus resemble the teeth described by the Van Hoepens, but the identity of the Van Hoepens' species with *T. meadowsi* remains somewhat doubtful.

Upper and lower second molars recovered by Broom from the Sterkfontein group of caves show characters similar to those of *Phacochoerus*, but the teeth are larger and more like those of *Mesochoerus* (below). The uppers are about 30 mm. long by 20 mm. broad and the lowers 35 mm. long and 15 mm. wide.

Tapinochoerus modestus Van Hoepen and Van Hoepen.

Tapinochoerus modestus Van Hoepen and Van Hoepen, 1932: Pal. Nav. Nas. Mus. Bloemfontein, ii, pp. 58–59, figs. 65–71.

Notochoerus broomi Shaw and Cooke, 1941: Trans. Roy. Soc. S. Afr. xxviii, pp. 295–296, fig. 1.

Type: Pair of upper third molars (fig. 16). Nas. Mus. C. 576.

Locality: Cornelia, O.F.S.

Horizon: Cornelia Deposits.

Dimensions:

	RM^3.	LM_3.
Greatest length:	62·0 mm.	51·0 mm.
Greatest height:	53·0 mm.	47·0 mm.
Occlusal breadth:	14·5 mm.	12·6 mm.

Paratype: Lower left third molar (fig. 16).

Dimensions: See above.

This small species resembles *T. meadowsi* in structure but is a good deal smaller. There are about five or six pairs of lateral columns and six or seven simpler median columns. The anterior columns are rather folded and the posterior ones simple. The teeth are hypsodont and the general form is similar to *T. meadowsi*, but the columns are a little more widely separated.

The species "*Notochoerus*" *broomi* erected by Shaw and the writer on a supposedly lower third molar (fig. 17) from the Vaal River gravels (Arch.

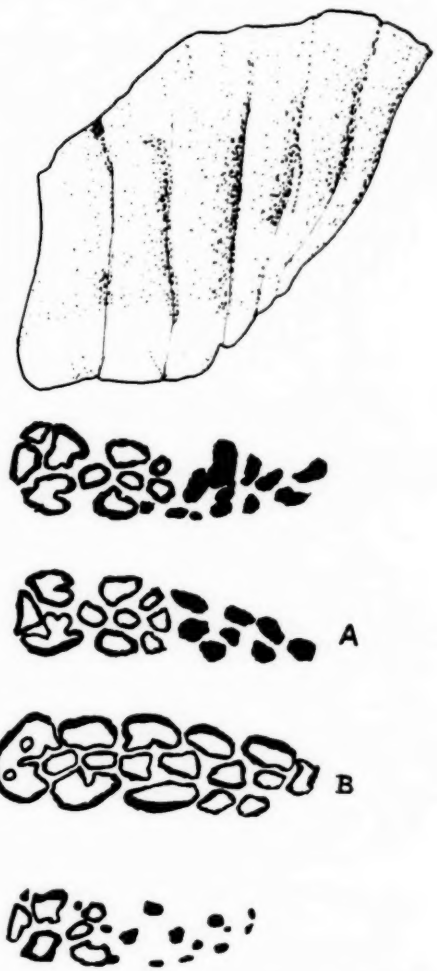


FIG. 16.—*Tapinochoerus modestus* Van Hoepen and Van Hoepen. *Above*: Enamel pattern and lateral view of type upper right third molar. *Centre*: (A) Enamel pattern of upper left third molar. (B) Enamel pattern of section through type upper left third molar viewed from below. *Below*: Enamel pattern of type lower left third molar. All natural size. (Redrawn from Van Hoepen and Van Hoepen.)

Sur. No. 35) appears on re-examination to be a left upper tooth falling within the Van Hoepens' species. Its dimensions are:

Greatest antero-posterior length (as preserved): 32 mm.
Width of anterior group of columns: 15·5 mm.
Height of second lateral column: 42 mm.

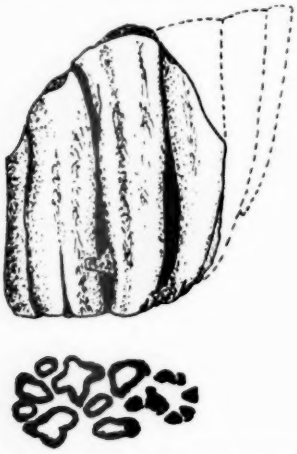


FIG. 17.—Occlusal and lateral views of referred upper molar of *Tapinochoerus modestus* Van Hoepen and Van Hoepen, formerly the type of *Notochoerus broomi* Shaw and Cooke. Natural size. (From Shaw and Cooke, modified in restoration.)

That this is definitely a smaller species than *T. meadowsi* and not merely an early stage of eruption is shown by the manner in which the crown comes into wear, so that at corresponding stages of eruption it presents the same aspect as *T. meadowsi* but is only two-thirds as large.

A section cut by Van Hoepen through the type left upper molar shows a pattern very like that of *Phacochoerus* and there can be little doubt that these species are not very remotely connected.

Genus MESOCHOERUS Shaw and Cooke.

Genotype: *Mesochoerus paiceae* (Broom).

Large pigs possessing third molars with moderately high columns and early root formation. The lateral columns are distinct and widely separated, uniting only at their bases and being demarcated from the roots by a distinct and well-developed cingulum. The columns are arranged after the *Notochoerus* pattern with pairs of laterals separated by smaller median columns.

Very possibly this genus may be reduced to a sub-genus of *Notochoerus*.

Mesochoerus paiceae (Broom).

Notochoerus paiceae Broom, 1931: Rec. Albany Mus. iv, pp. 167–168, fig. 1.

Mesochoerus paiceae Shaw and Cooke, 1941: Trans. Roy. Soc. S. Afr., xxviii, pp. 293–295, pl. liv. (1 and 2).

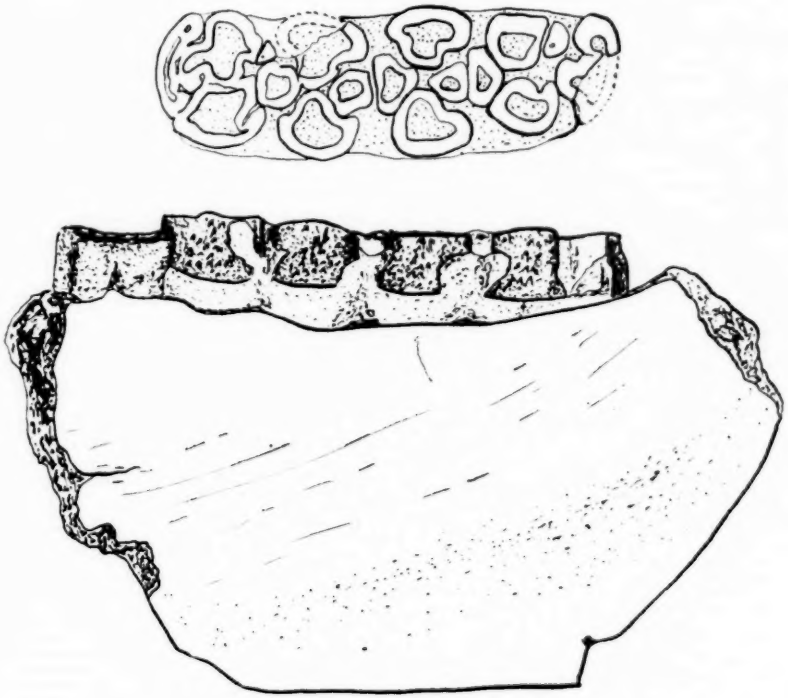


FIG. 18.—Occlusal and lateral views of type third lower molar of *Mesochoerus paiceae* (Broom). Natural size. (Original.)

Type: Broken lower jaw with right third molar *in situ* (fig. 18). M.M.K. No. 4088.

Locality: Windsorton, Kimberley District, C.P.

Horizon: Vaal River gravels.

Dimensions:

Greatest width of jaw-bone: 47mm.

Dimensions of Third Molar (much worn):

Greatest length:	70 mm.
Anterior width:	23 mm.
Median width:	22 mm.
Height of posterior columns:	12 mm.

Neotype:

Broken right mandible with incomplete second to fourth premolars and first molar, and well-preserved second and third molars (fig. 19).

Locality: Pniel Estate, near Barkly West, C.P.

Horizon: Probably Younger Gravels of the Vaal River.

Dimensions:

	Greatest width of jaw-bone:	38 mm.
Second molar:	Greatest length:	32 mm.
	Width across anterior columns:	19 mm.
	Height of crown:	14 mm.
	Length of roots:	20–25 mm.
Third molar:	Greatest length:	68 mm.
	Width across anterior columns:	22 mm.
	Height of anterior columns:	34 mm.
	Height of posterior columns:	31 mm.
	Length of anterior roots:	14 mm.

In his description of the type Broom states that "there are four large lateral cusps with five small median cusps, a small flattened anterior cusp and apparently a single folded posterior cusp. Though the grinding surface is like *Notochoerus capensis* and *N. meadowsi*, the cusps in this new form differ in being manifestly very much less hypsodont. The bases of the cusps are seen and immediately above the bases the cusps are very distinctly separated from each other as shown in the figure."

The type specimen, while giving an excellent picture of the pattern of the third molar in wear, gives no idea of the actual height of the crown. The slightly less massive jaw of the neotype contains a third molar which is almost fully erupted as its anterior columns are above the level of the abraded second molar but the third molar is unworn, presumably as a result of mal-occlusion. The bone of the jaw has been removed to expose the entire tooth, which is described by Shaw and Cooke as follows: "The crown is made up of four pairs of lateral columns and seven median columns, the first and last of the median columns occupying the anterior and posterior extremities respectively. The columns are all of much the same height (approximately 32 mm.) and at the base of the lateral columns there is a pronounced cingulum. The lateral columns terminate by means of roots, which are strongly developed on the first and second pair of columns."

The neotype thus shows the characteristic low-crowned nature of the

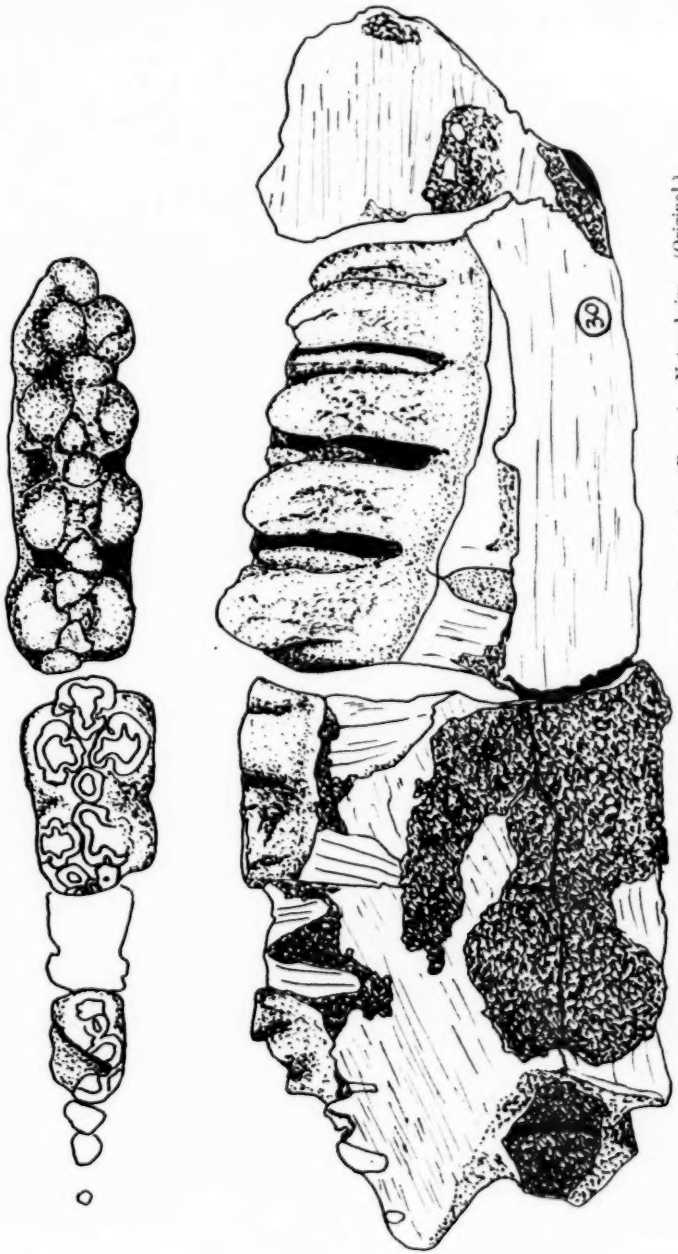


FIG. 19.—Occlusal and lateral aspects of neotype jaw of *Mesochoerus paiceæ* (Broom). Natural size. (Original.)

third molar, as anticipated by Broom, and the arrangement of the columns is such that at the same stage of abrasion the neotype would certainly show a pattern very like that of the type. The third molars of this species differ from those of *Notochoerus* in being considerably less hypsodont; in having lateral columns which are clearly separated from one another and in possessing a cingulum which demarcates them from the roots. The roots themselves are larger than in *Notochoerus* and are of the brachyodont type.

The second molar of the neotype has two pairs of lateral cusps, a flattened anterior cusp with several small conelets upon its apex, two median cusps between the lateral pairs and a posterior cusp of greater size and more complex shape. The lateral and posterior cusps are each somewhat "trilobate" in form. There are four long roots. This tooth is a little larger than the stump in the jaw of the type. A second molar from Sterkfontein has been doubtfully referred to this species (Broom, 1936).

The first molar also has four roots, but its crown pattern is unknown. The fourth premolar is either four-rooted or has two wide and partly divided roots. Its crest appears to have comprised three cusps more or less in line. The third premolar was a small two-rooted tooth, but its crown pattern is unknown.

Shaw and the writer suggested that this genus might have affinities with the forest-pig *Hylochoerus* of Central Africa, but this possibility has been doubted by Leakey (1942, 1943) who suggests a greater similarity to *Potamochoerus*.

Discussion.

East African Suidae.

Several species of fossil Suidae have been described by Dr. L. S. B. Leakey (1942, 1943) from deposits in East Africa, and these fossils bear striking resemblances to the South African forms. Unfortunately it has not been possible for the writer to examine the East African material, but Dr. Leakey has very kindly provided casts of some of the third molars characterising the more important types and these have been compared with our specimens so that a few comments may not be inappropriate.

In his 1942 paper Leakey described eight species from the old lake deposits of Oldoway Gorge at the south-east corner of the Serengeti Plains, Tanganyika Territory. These beds are referred to the middle Pleistocene and are associated with Stone Age cultures ranging from Pre-Chellean at the base to Acheulean Stage VI at the top. In addition to material which cannot be distinguished from the living *Phacochoerus*, he describes an extinct species *P. complectidens* which is distinguished by a large number of medial pillars arranged in a complex fashion. A large phacochoere possessing elongate Y-shaped lateral pillars is considered to warrant generic distinction

and is described under the name *Afrochoerus nicoli*. A single tooth is referred to the extinct *Sus limnetes* originally described by Hopwood (1926 B) from the Kaiso beds of Uganda, and other fragmentary teeth are referred to Hopwood's genus *Metridiochoerus*. A further species originally described by Hopwood (1934) from Oldoway, *Potamochoerus majus*, is also represented. A new species of *Mesochoerus* is described under the name *M. olduvaiensis* and material is ascribed to Hopwood's (1934) very inadequately described *Notochoerus dietrichi* from Oldoway.

In his 1943 paper Leakey describes fossil Suidae from beds on the banks of the Omo River in Southern Abyssinia, and it is suggested that the Omo fauna is of Lower Pleistocene age. No human artifacts have been found, however, and the age is not certain. *Sus limnetes* is again recorded and another new species of *Mesochoerus*, *M. heseloni*, is described. Two large species of notochoere form the basis for the erection of new genera, *Pronotochoerus* and *Gerontochoerus*, typified respectively by *P. jacksoni* and *G. scotti*.

There are thus described from the two sites the following species:—

Sus: *S. limnetes*.
Potamochoerus: *P. majus*.
Phacochoerus: *P. africanus* (or *aethopicus*), *P. complectidens*.
Afrochoerus: *A. nicoli*.
Metridiochoerus: *M. sp.*
Mesochoerus: *M. heseloni*, *M. olduvaiensis*.
Notochoerus: *N. dietrichi*.
Pronotochoerus: *P. jacksoni*.
Gerontochoerus: *G. scotti*.

Sus limnetes appears to be a valid and rather widespread East African species, having now been recorded from the type locality at Kaiso and also from Oldoway and Omo.

Potamochoerus majus is only known from Oldoway, but seems to be quite distinct from the living *P. porcus*, being larger and having a slightly different arrangement of the columns. The remaining member of the pig family with low-crowned teeth of the "cusped" type (*Hylochoerus*), as opposed to those with "columnar" teeth, is not represented amongst Leakey's material. It has supposedly been recorded from Kaiso by Hopwood as *Hylochoerus euilus*, but from Hopwood's figure it seems probable that his species belongs rather to a member of the *Notochoerus* or the *Mesochoerus* group and not to *Hylochoerus* at all.

The phacochoere which Leakey calls "*P.* cf. *aethiopicus*" is reported to have well-developed roots and may be *P. africanus*. His species *P. complectidens* is very similar to some teeth of the South African *P. compactus*,

but a good deal wider than any of our specimens and approaches ***P. altidens*** in this respect. The lateral columns, however, are much less elongate than is the case in the latter species. More adequate material than the fragmentary type of ***P. complectidens*** is required before much can be said concerning its relationship.

The validity of the genus *Afrochoerus* is, as the present writer and Wells (1945) have already pointed out, somewhat doubtful. The main grounds for the creation of the genus is the presence of elongate Y-shaped lateral columns, but this feature does not constitute a satisfactory criterion for distinction from *Phacochoerus* and especially not in teeth as worn as the type. It is observable in living phacochoeres that the longer teeth have more elongate lateral columns and the shorter teeth more rounded ones, so that it appears natural for large teeth of this genus to show flattened laterals. Leakey has further suggested that our ***P. altidens*** might be included in *Afrochoerus*, but if a generic distinction is to be considered it appears that the Van Hoepens' *Stylochoerus* would have priority. While more material of Leakey's species is awaited in order to determine the characters shown in little-worn teeth, it seems that the generic distinction from *Phacochoerus* is not really justified even if the specific distinction is necessary. "*Afrochoerus*" *nicoli* is founded on lower teeth, and it is suggested that *Phacochoerus complectidens* may represent the upper dentition of ***P. nicoli***.

The new species of *Mesochoerus* are certainly specifically distinct from *M. paiceae* of South Africa and from each other. They are of particular interest in showing the apparently widespread and varied nature of this genus which in many respects appears to provide a link between the "cusped" teeth of the pigs and the "columnar" teeth of the wart-hogs. *M. heseloni* is very low crowned and the molars have long roots, while the fourth premolar is less molariform than in the genotype, so that this species appears to be the most primitive member of the genus so far recorded.

As far as Leakey's material of *Notochoerus dietrichi* is concerned, it can be stated that the cast of the fine unworn lower molar is absolutely indistinguishable from corresponding teeth of Broom's (1928) "N." *meadowsi*. If it does in fact represent Hopwood's inadequately described species from the same locality, "*N.*" *dietrichi* is undoubtedly a *Tapinochoerus* as now understood and most probably is a synonym of *T. meadowsi*. Further, since Hopwood emphasises that "*N.*" *dietrichi* is "a *Notochoerus* with smaller and less complicated *upper* molars than the genotype *Notochoerus capensis*," this provides a measure of further confirmation of the distinctness of *N. capensis* and *T. meadowsi*.

Pronotochoerus jacksoni has only three pairs of lateral columns and possesses well-developed roots even before the posterior part of the tooth is fully erupted. It seems very possible that, as Leakey suggests, this

approximates to the ancestral state for the true *Notochoerus* in which root development is somewhat delayed. *Gerontochoerus scotti* has a larger number of lateral columns (six to eight) in the third molars, while retaining primitive roots. From the cast supplied by Leakey it looks very much as if the upper third molar owes its size and complexity to fusion of two tooth elements, for the anterior two pairs of columns are rooted separately from the posterior part of the tooth and they appear almost distinct from the hinder elements. If this is indeed the case, the genus warrants very close and extensive study, for it may well be a real example of the hypothetical processes which have been inferred to account for the complexity of certain types of molars. The existence of Leakey's excellent material makes it the more regrettable that closer comparison with *Notochoerus capensis* is prevented by the fact that the South African species is so far known only by a single imperfect tooth. There is no doubt of the intimate relationship between Leakey's new genera and *Notochoerus*, and it would seem that further material from South Africa is required before the precise degree of connection can be elucidated. Undoubtedly great profit would be gained by actual direct comparison of all the East African and South African material.

Evolution of the African Suidae.

With the discovery of *Mesochoerus*, now represented by three species, and of the important new East African forms, a somewhat clearer picture of the relationship between the "cusped" teeth of the pigs and the "columnar" teeth of the wart-hogs seems to be emerging. While none of the genera and species so far known from Africa, however, can be an ancestral type in itself, *Mesochoerus* seems to provide an important link between *Potamochoerus* and *Notochoerus*. *Mesochoerus heseloni*, the most primitive species of this genus yet found, is presumably not very far removed from the form of a common ancestor from which *Potamochoerus*, *Sus*, and *Hylochoerus* developed in a conservative direction and *Phacochoerus* and the Notochoere group in a more progressive direction.

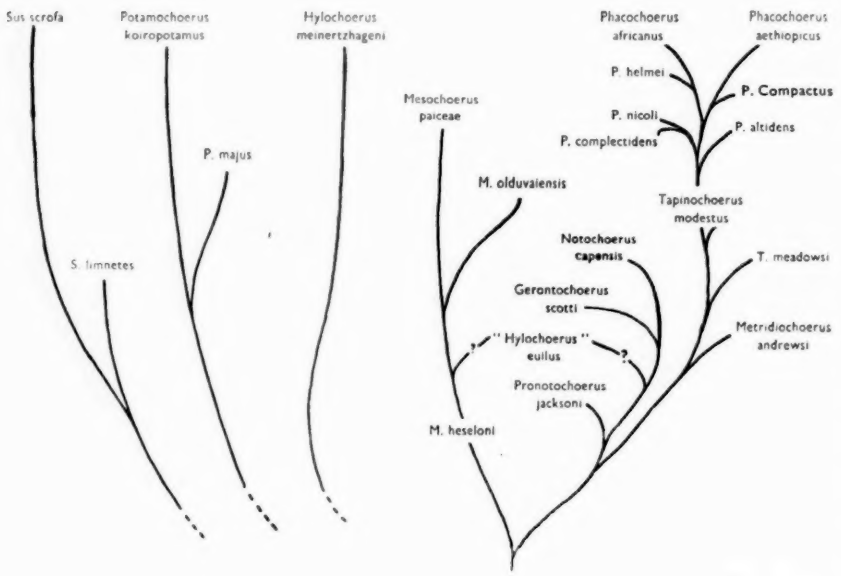
Pronotochoerus and *Gerontochoerus*, with their combination of high crowns and well-developed roots seem to be closely allied to *Notochoerus* and are branches off a line trending through *Tapinochoerus* towards the Phacochoeres. Both are much too large to represent actual ancestral types, but the small *Tapinochoerus modestus* of South Africa is remarkably like *Phacochoerus* and must be very close to the form of their common ancestor, while *T. meadowsi* is a larger branch form derived from more remote ancestors. There has probably been a good deal of convergent development amongst the extinct forms.

Colbert (1935) has given in his "Studies on Indian Fossil Mammals" an excellent phylogeny of the Suidae of India. In his diagram he apparently

derives *Potamochoerus* through a *Propotamochoerus* of the Dhok-Pathan (Upper Pliocene) from an unknown ancestor of the Kamlial (Upper Miocene). The *Sus* branch is thus considered to have separated from the *Potamochoerus* ancestor in Miocene times. The *Phacochoerus* branch, on the other hand, is indicated by him as separating only about the Tatrot zone (Uppermost Pliocene) and is considered to have developed through the Pleistocene *Sus falconeri*. While this possibility cannot be ignored, it would appear that the African fossil *Mesochoerus* is indicated as lying very close to the direct line of ascent of *Phacochoerus* and also indicates a closer relationship with *Potamochoerus* than would be inferred from Colbert's paper. It does not seem unreasonable to suggest that the living African genera *Potamochoerus* and *Hylochoerus* may have had a more purely African evolution than is suggested by Colbert, while *Sus* may have separated as he has indicated. *Sus falconeri* then becomes a convergent type and not an ancestral one.

An attempt is made here to give in diagrammatic form the present writer's concept of a possible relationship between the various species so far known from South and East Africa. While the branch culminating in *Phacochoerus* seems fairly clear, the connection between this branch and the other living African forms remains obscure.

POSSIBLE PHYLOGENY OF THE QUATERNARY SUIDAE
OF SOUTH AND EAST AFRICA



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A REPORT ON THE CULTURE OF THE SOUTH AFRICAN CLAWED FROG *XENOPUS LAEVIS* (DAUDIN) AT THE JONKERSHOEK INLAND FISH HATCHERY.*

By D. Hey, D.Sc.

(Read November 20, 1946.)

Introduction.

In addition to its manifold uses in educational institutions, the South African clawed frog *Xenopus laevis* has achieved great prominence in scientific laboratories throughout the world as a test animal for early pregnancy. In consequence, the demand for these animals has been so great that supplies from natural sources are being rapidly depleted in the Cape Peninsula and its precincts. The disappearance of *Xenopus* is being accelerated still further by the introduction of the predaceous American Largemouth Bass (*Huro salmoides*) into their natural habitat—the vleis and dams of South Africa.

This danger was appreciated by Dr. Louis P. Bosman, one of the pioneer medical scientists in the use of *Xenopus* for pregnancy tests. With a view to ensuring adequate supplies of these animals, he prevailed upon the Cape Provincial Administration to sponsor research on the artificial cultivation of *Xenopus* at the Jonkershoek Inland Fish Hatchery near Stellenbosch, Cape, South Africa.

Whereas in the past "wild frogs" were collected, sexed, and freighted under primitive conditions, thanks to the foresight of Dr. Bosman, this Hatchery now provides facilities not only for breeding *Xenopus*, but also for grading, conditioning and shipping them under optimum conditions. Whereas neither the cultural technique has been perfected as yet, nor have frogs been produced in anything like sufficient numbers, yet it is considered that sufficient information of value to would-be breeders of *Xenopus* has been accumulated to warrant this publication.

* Dedicated to the Memory of Mr. D. Blignaut, my companion on many collecting trips.

General Description.

A number of excellent reference works on the anatomy and physiology of *Xenopus laevis* are available. The following general description, therefore, contains chiefly information relevant to the artificial cultivation of these animals.

The South African clawed frog, commonly known as the "platanna", belongs to the Pipidae, a rare family of the Anura, the six genera of which are confined to the African and South American regions. *Xenopus* occurs in Southern and Central Africa only, a fact which may prove of significance in delimiting the countries where it will be possible to culture them artificially. It inhabits almost any type of permanent water, chiefly dams, vleis, pans and, to a lesser extent, rivers and streams. A vlei or pan may be defined as a permanent or semi-permanent sheet of water, varying in depth according to the topography, the major portion of which consists of shallows with a luxurious growth of aquatic vegetation both submerged and emergent. A farm dam, on the other hand, is man-made, and varies greatly in size and depth.

Xenopus are usually found in great numbers in farm dams receiving the "run off" water from stables, or those carrying ducks. This is accounted for by the fact that such dams are comparatively rich in plankton and insect life, on which the frogs and their larvae feed. The factors governing their choice of certain dams in preference to others, however, has yet to be explained. For example, they may be very numerous in one dam and absent from the adjoining one, although the two appear identical. It has been noticed, however, that they favour discoloured water.

Xenopus, contrary to general belief, is wholly aquatic, except for occasional treks from water to water. It lives its entire life underwater, rising to the surface only to breathe. A dam containing *Xenopus* is consequently readily distinguishable by the animals breaking surface. This occurs less frequently in winter than in summer, because metabolism is slowed down by the lower water temperature and the colder water contains more oxygen. A certain amount of oxygen is absorbed through the skin and therefore, during winter, they remain submerged for long periods. On the other hand, during summer, submersion for more than half an hour may result in death. Consequently, when collecting by means of traps it is essential that these be lifted at least every half-hour.

Xenopus also rise to the surface when the "atmosphere is depressed", as for example before an impending thunderstorm. In the latter instance the animals lie on the surface of the pond, their eyes and nostrils just protruding. At the slightest disturbance they all disappear.

An average platanna measures 16·5 cm. from the tip of the out-

stretched hind legs to the snout, the body-length being 7·5 and the weight 50 gm.

Occasionally large females up to 13 cm. in body-length and weighing 210 gm. are found, but these are rare. The condition of the frogs in any water depends largely upon the numbers present in relation to the food supply. Many dams contain numerous frogs but none exceed 30–40 grammes, and all are in poor condition. Others contain a relatively small number of frogs, the females averaging well over 100 gm., with a fair proportion up to 200 gm.

In contrast to other frogs the three inner toes of the hind feet are provided with claws, which, however, would appear to be of little value for offence or defence. The hind legs are powerful, the feet being webbed, and are used both as swimming and balancing organs and for propulsion on land. In either medium the platanna jumps forwards or backwards with apparent ease. The body is tapered from back to front and flattened dorsoventrally; it is protected by a very thick, slimy skin containing numerous mucous glands. The secretion from these glands not only makes handling difficult but is sufficiently poisonous to render the frogs distasteful to most predators. For example, it will cause a dog to foam at the mouth. Nevertheless these frogs are eaten by some predators, including pigs, ducks and Largemouth Bass (*Huro salmoides*). The latter, however, prefer the immature stages, the adults being taken only when the fish is hungry.

The dorsoventral flattening, slippery skin and pliable skeleton enable the platanna to pass through an unbelievably small opening, as anyone who has tried to hold them in captivity learns to his sorrow. A specimen of 5·0 cm. in body-length (13·5 gm.) will pass through wire-netting of half-inch mesh, while a horizontal slit of half-an-inch is negotiated by a 7·5 cm. specimen with ease.

In order to confine them at Jonkershoek, ponds are enclosed with a 24-inch-high fence of half-inch mesh bird wire, with the upper two inches bent over to form a veranda. The lower six inches of the fence is covered with galvanised iron to prevent the smaller animals from escaping.

The coloration of the "wild" frogs differs with locality, and may vary from dark brown to pale grey. Whatever the dominant colour, however, all specimens are mottled with black against the background of brown-yellow, green-blue, or grey, as the case may be. All specimens are dirty white on the under side. While skin colour is to a certain extent associated with the environment in which the frogs live, it is doubtful whether it serves the purpose of protective coloration to any major degree, as there is often a wide range in colour of specimens collected from any one dam. In any case the water is so discoloured in the majority of dams that the animals are well concealed.

The forelegs are small and provided with long soft fingers. They are used chiefly for amplexus, climbing and feeding. Large particles of food are pushed into the mouth with rapid jerky movements of the forelegs.

The eyes are wide-set, small and beady, somewhat raised above the head. Eyesight is sharp for an aquatic animal, and there is an almost instantaneous reaction to movement up to a distance of thirty feet. The nostrils are set close together near the margin of the snout. The sense of smell is very acute, which incidentally is the reason why they are so easily caught in conical traps baited with raw meat.

For a lower vertebrate, the platanna possess a highly developed instinct, if not actually a certain degree of intelligence. This possibly somewhat startling claim is made on the basis of many years of careful observation of their ways, and is evidenced by their reactions to varied situations. They are most ingenious in entering carefully protected fish-fry tanks at the Hatchery and display equal versatility in escaping from captivity. When a pond or dam is being emptied they leave it overnight, and unerringly make their way to more permanent water. There can be no doubt that *Xenopus* wander at night, for they have never been observed on the move in the day and yet they will make their appearance in a daphnia tank as soon as the algal culture matures.

Xenopus frogs feed on animal food, both invertebrate and vertebrate, such as *crustacea*, insects, worms, tadpoles, small frogs, fish, etc.

In the Western Province breeding normally takes place in the late winter or early spring, which may be any time from August onwards. At this season some frogs may leave the permanent waters and migrate to the temporary marshes and vleis, while others breed in their home water.

At this season the female is distended with ova and the genital flaps are swollen. The male, who is normally silent, becomes vocal at this time of the year, and prior to mating his croaks become more and more pronounced, but not nearly as audible as those of *Rana*. He clasps the female in an inguinal amplexus during the entire spawning act. Egg-laying, however, occurs only after a few hours of amplexus, the eggs being laid singly at frequent intervals. As these pass the male cloaca they are fertilised and, being sticky, adhere to the aquatic vegetation. As the frogs swim about during the spawning act the eggs are scattered over a fairly wide area. This has the effect of reducing losses from predators.

The number of eggs shed at any individual spawning may vary from a few hundred to a thousand or more. In addition a female may spawn a number of times during the season. Despite the fact that the eggs are shed singly, however, they are not all fertilised. After the swelling of the mucilaginous coat the eggs measure approximately 3 mm. in diameter.

At the normal water temperature during this season (60°–65°F.) the

eggs hatch in about three days. For the first few days thereafter each larva remains attached to weeds and derives its nourishment from the yolk-sac. With the development of the alimentary canal the tadpole becomes free-swimming and rapidly assumes its characteristic shape. The head broadens, the eyes become large and prominent, and two maxillary tentacles appear near the lateral edge of the mouth. Suspended in the water with the head down, and the tip of the tail rapidly vibrating, they gulp away continuously, ingesting microscopic food, chiefly the phytoplankton. Where zooplankton is plentiful this is also consumed, and forms as large as *Daphnia magna* have been taken from the gut of tadpoles. Despite the claims of many workers, including Bles (1905), that *Xenopus* feeds exclusively on algae, it has been our experience at the Hatchery that the larvae are non-selective in diet, automatically consuming all plankton ingested. Where food is plentiful the larvae grow rapidly, sometimes attaining a length of 9 cm. When food is less plentiful they may metamorphose when much smaller. Metamorphosis commences with the appearance of the hind legs, after which the front legs appear. At this stage the tail begins to shrink, and when all the limbs are fully developed the animals commence life on the bottom. They feed on daphnia and a variety of small larvae, gradually passing to larger and larger food items. They become sexually mature between the second and third year, depending upon the food supply. Large females of 200 grammes and over are considered to be at least five years old, but no information on their longevity under natural conditions is available as yet. That they are long-lived, however, is evident from the fact that they have been kept in aquaria for fourteen years (Flower, 1925 and 1936).

Artificial Cultivation.

After studying all available literature on the subject, it was presumed that the cultivation of *Xenopus laevis* under hatchery conditions would prove difficult if not well-nigh impossible. Consequently the first experiments were confined to determining an artificial method for inducing these animals to breed. Selected pairs of frogs were injected with varying quantities of natural and artificial stimulants, including pregnancy urine extract prepared according to Shapiro and Zwarenstein, pituitary extract, and certain analogous products. The frogs were placed in battery jars, 20 cm. × 20 cm. × 50 cm., filled to a level of 23 cm. Efforts were made to vary the conditions in the tank, such as pH and temperature. The beneficial effect of falling water as described by Bles (1905) was also tested. With the exception of injections of Prolan, which caused amplexus, in no single instance was a positive result obtained.

At the time when these experiments were in progress great attention was being devoted to the culture of *Daphnia magna* at the Jonkershoek Hatchery. The principle involved in the culture of *Daphnia* is to engender a growth of algae and infusoria in concrete tanks by the application of various combinations of organic and inorganic fertilisers. As soon as the water "greens" the culture tanks are "seeded" with individuals of *Daphnia magna*. It was noticed that, as soon as the culture in a tank matured, *Xenopus* appeared in them and in every instance spawned.

In view of the fact that all efforts to induce spawning in *Xenopus* by artificial means were abortive, and furthermore that it had by no means been established that ova produced in that way at Jonkershoek would be viable, research was now directed to inducing the frogs to spawn by natural means. Using the same-sized containers, and one gallon of culture medium per jar, pairs of frogs were placed in a variety of media such as are usually used for *Daphnia* culture. Results, however, were negative.

A concrete tank, $308 \times 6 \times 3$ ft., was fertilised with three quarts of sheep manure and one quart of superphosphate of lime, and as soon as the water "greened" 20 pairs of breeders were introduced. Within ten days free-swimming larvae were seen and after a month the tank was well stocked. This experiment was repeated during the summers of 1940 and 1941 with equal results.

The number of frogs which can be produced under such conditions, however, is limited, and consequently it was desired to test this method on a large scale. This, however, was not possible at the time, due to the lack of suitable ponds.

Two such ponds, enclosed with a frog-proof fence, were eventually completed in August 1945, and brought into use immediately. Results were most gratifying and it may now be claimed that it is possible to cultivate *Xenopus* in captivity, utilising either earth ponds or concrete tanks. A general description of the methods employed at this Hatchery follows.

Prior to the breeding season the pond is drained, cleaned, and fertilised with a mixture of kraal manure, compost and superphosphate of lime (16 per cent. water-soluble). This is spread lightly over the entire pond bottom and raked into the soil. The pond is then filled and allowed to mature, only sufficient water being allowed to enter to compensate for seepage and evaporation. When the water has greened it is seeded with *Daphnia magna* to ensure an adequate food supply. Equal numbers of well-conditioned males and females are then introduced at the rate of 200 per acre. In addition to the natural food present, the frogs are fed on minced liver at defined feeding spots twice weekly. Overfeeding is to be preferred to underfeeding, as well-fed frogs are less likely to prey on the larvae than underfed

ones. Unless overfeeding is excessive there is no danger of pollution, since any unconsumed food will decompose and add to the plankton. Whenever the water begins to lose its green coloration more fertiliser must be added. This is usually done by dumping bushel baskets full around the perimeter in the shallow water at ten-yard intervals.

As already stated, breeding commences in early spring and, provided that an adequate supply of green water is maintained, will continue at intervals throughout the summer. Not only do individual females differ in their time of spawning, but a well-conditioned female may spawn as many as three times. Consequently the removal of breeding stock during the summer is optional, the disadvantage of their presence being that they will consume numbers of larvae. On the other hand, provided that they are well fed, losses from cannibalism should be proportionately small. When the first crop of fry has metamorphosed, artificial feeding with finely minced liver is commenced, gradually increasing the size of the food particles as the animals grow.

In autumn the adults are removed from the breeding pond and returned to the stock tanks. This is done by means of conical traps baited with liver and set at the feeding spots. Feeding is naturally discontinued at this stage. This type of trap has been found very effective and will catch the majority of breeders. The use of nets is not advocated until such time as all the larvae have metamorphosed. *Xenopus* larvae are very delicate and cannot be handled or netted. The metamorphosed form, however, is more hardy and will pass through the meshes of the net without injury.

With the adults removed, the feeding of the developing *Xenopus* is continued, the optimum growth rate recorded to date being 4 cm. body-length at first year and 6½ cm. at second year. When the requisite size has been attained they are removed to the breeding ponds for sorting and distribution.

From the breeding ponds these frogs are transferred to concrete holding tanks for sorting and grading. They are first sexed, mature females being recognised by the genital flaps. The females are then graded into four sizes, viz., 200 grammes, 100 grammes, 40 grammes and immature forms. These latter are returned to the rearing ponds and the graded females and the males are placed in their respective holding tanks prior to despatch. In these tanks feeding is continued.

All sexing and grading is done by hand, since automatic graders have been found unsatisfactory. Once the method of differentiating the sexes has been mastered, hand sexing and grading is not excessively slow. Whereas an inexperienced man has great difficulty in handling *Xenopus*, an experienced person can grade them quickly and with ease. The success depends upon the manner in which the frogs are held. *Xenopus* should never be

grasped too firmly as the harder one holds them the more they struggle and the more slippery they become. Rapid, jerky movements also unsettle them. At Jonkershoek the method employed in sorting is as follows:— The frogs are dipped from the holding tank by means of a square hand net into a large shallow white enamel basin. From this basin the frogs are sorted by slipping the hand under each frog with a deliberate and steady movement. The frogs are not grasped, but merely lifted from the basin and dropped into the respective holders. If, for some reason or other, it is desired to hold a frog, the best method is to lift it in the palm of the hand with the head facing the wrist, and it should be gently grasped between the thumb and second finger in the inguinal region, the first finger passing between the hind legs, which then hang free.

The sorted frogs are placed in their respective holding tanks prior to despatch, which should be within a reasonably short time of sorting. It has been found possible to hold as many as 5,000 large females in a tank 20×6 ft. and 3 ft. deep, provided with a flow of water from a half-inch pipe for as long as three to four weeks. It must be stressed, however, that they require almost constant attention to prevent fouling of the water and to observe any occurrence of parasitic or skin diseases, which spread rapidly and soon assume epidemic proportions.

For shipment by rail, where the journey does not exceed five days' duration, standard five-gallon carboys are used, placing 300 frogs in each. These metal containers are boxed to insulate them against excessive fluctuations in temperature, and are painted inside with bituminous paint to prevent metal-poisoning. The frogs should not be fed for at least three days before transit, to minimise fouling of the water.

For overseas shipments a squatter type of container is employed, to allow a larger surface area per frog. These are 27 inches in diameter, and 125 animals have been carried in each for journeys of up to three months' duration under trying war-time conditions. Accompanied by a technical officer, however, and shipped under cover, it is possible to carry double the number of frogs. The following list of instructions is usually issued to the person taking charge of the consignment:

(1) Fill containers to shoulder-level.

(2) Examine daily and remove any dead specimens.

(3) Change the water at least once a week, using only fresh water for the purpose.

(4) Feed twice weekly on chopped meat the size of a threepenny-piece, allowing approximately two pieces per animal.

Diseases.

It is very important that *Xenopus* be kept in favourable quarters, not unduly overcrowded and well fed, nor should they be held for more than six months in concrete tanks, no matter how carefully attended, or they will drop off in condition. A stream of water must pass through the tanks and any unconsumed food and other detritus be removed regularly. Under normal conditions disease is rare, and the animals, if infected, are able to withstand the ravages of the pathogen. Should they commence dying in large numbers, however, immediate action is essential. All frogs must be removed from the tank and the infected specimens isolated. The tank should then be disinfected with quicklime, thoroughly washed, refilled, and the healthy animals replaced. If the disease can be diagnosed, and the treatment thereof is known, a fair percentage of infected specimens can be saved. If not, it has been our experience that it is wiser to kill all diseased animals, as this often prevents the disease from assuming epidemic proportions.

The following are the commoner diseases experienced at Jonkershoek to date.

Intestinal Cestode.—Tapeworms are found in nearly all *Xenopus*. If present in large numbers a falling off in condition ensues, but in general they do not appear to have any effect upon the animals.

Skin Parasites.—Skin parasites spread very rapidly when the animals are kept under crowded conditions, particularly a species of *Hirudinea*. These eventually cause open sores on the frogs, which soon develop big cottony tufts of *Saprolegnia sp.* The parasites can be killed by immersing the frogs for a few minutes in a very weak formalin solution. The *Saprolegnia sp.* and the open sores are cured by weak salt-baths.

Conclusions.

The shortcomings of the foregoing account are evident, and the need is appreciated for further research on aspects such as optimum living conditions for the frogs, their longevity under semi-natural conditions, diseases and range of food items. For practical purposes it will be necessary to determine growth rates and feeding costs in order to arrive at an estimate of the cost of culturing these animals under hatchery conditions.

It is not anticipated, however, that any difficulties will be experienced in determining the foregoing and it is merely a matter of time before *Xenopus* can be cultured as easily as fish. Produced under optimum conditions, these hatchery-cultured frogs need be in no way inferior to wild animals. In fact they should be superior, in that they are in perfect condition and

disease-free. Universities and medical institutions will then be in a position to order frogs in sizes and quantities to suit their needs, whereas at present supplies from natural sources are unreliable and erratic.

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THE DEVELOPMENT OF THE VENOUS SYSTEM OF *XENOPUS LAEVIS*.

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(With 7 Plates (I–VII) and 11 Text-figures.)

(Read March 19, 1947.)

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Introduction.

This paper represents the fourth of a series published in this journal on the anatomy and development of the vascular system of *Xenopus laevis*.

Most of our knowledge of the Salientia or Anura is based on descriptions of *Rana*, which, if we accept Noble's classification (1922), is not in the typical line of the Salientia, but one of its more specialised members. The Pipidae, however, including the genera *Pipa*, *Protopipa*, *Hemipipa*, *Hymenochirus*,

Pseudohymenochirus and ***Xenopus***, are closer to the primitive stem of the Salientia, and might thus be expected to yield valuable information on the evolution of the group. Moreover, the importance of ***Xenopus*** as a laboratory animal in South Africa and its recent world-wide publicity since the discovery of the pregnancy test make any further knowledge of its anatomy a useful adjunct.

As stated in the first paper of the series (Millard, 1941) the object of the work was firstly to establish an accurate and detailed description of the vascular anatomy of both adult and young stages of ***Xenopus***, and secondly to determine whether any knowledge could be obtained therefrom as to the position of the Pipidae among the Salientia. Since this paper concludes the description of the anatomy and development of the vascular system, and since during recent years our knowledge of the rest of the anatomy has also been accumulating, a discussion is included at the end on the evidence which has emerged as to the nature and phylogenetic history of the group. Recent literature on the subject is also reviewed.

As far as the development of the venous system is concerned, recent accounts on ***Xenopus*** have been published by Paterson (1939 and 1942) and Weisz (1945). The former dealt only with the veins of the head region, and the latter included a very general account which is considered by the writer to be inaccurate in several particulars.

Several excellent accounts exist of the development of the veins of other Amphibia, particularly those of Hochstetter (1888, 1894 and 1906) on ***Salamandra*** and various Salientia, Kampmeier (1920) on ***Bufo***, and Shore (1902) and Engels (1935) on ***Rana***. In addition there are the full accounts of Gaupp (1896) and Francis (1934) on the adult anatomy of ***Rana*** and ***Salamandra*** respectively. Further work which has proved exceedingly useful is that of van Gelderen (1933), and Goodrich (1930) on the veins of the head, and O'Donoghue (1931) on abnormalities of the vascular system.

Material and Technique.

Methods of fixation, sectioning and staining were similar to those described in the previous paper (Millard, 1945), in fact many of the same series of sections were utilised. Graphic reconstructions were made by means of a Leitz "Panphot", which was also used for the drawing of the sections in text-figures 3 and 4, and plates IV to VII. The diagrammatic representations of development shown in text-figures 2, 5, and 6 were drawn free-hand, and though not to scale were based on graphic reconstructions. It was endeavoured to obtain as complete a series of stages as possible,

and altogether sections of the following sizes of tadpoles were studied (measurements taken from snout to end of tail before fixation): 4 mm., 5 mm. (three embryos), 6 mm. (three embryos), 6·5 mm., 7 mm., 8 mm. (two tadpoles), 9 mm., 10 mm., 12 mm., 14 mm., 18 mm., 24 mm., 31 mm., 37 mm., 44 mm., tadpole with four legs before onset of metamorphosis, tadpole just commencing metamorphosis, tadpole half-way through metamorphosis, and a young frog just after the completion of metamorphosis.

Development of the Omphalomesenteric and Hepatic Portal Veins.

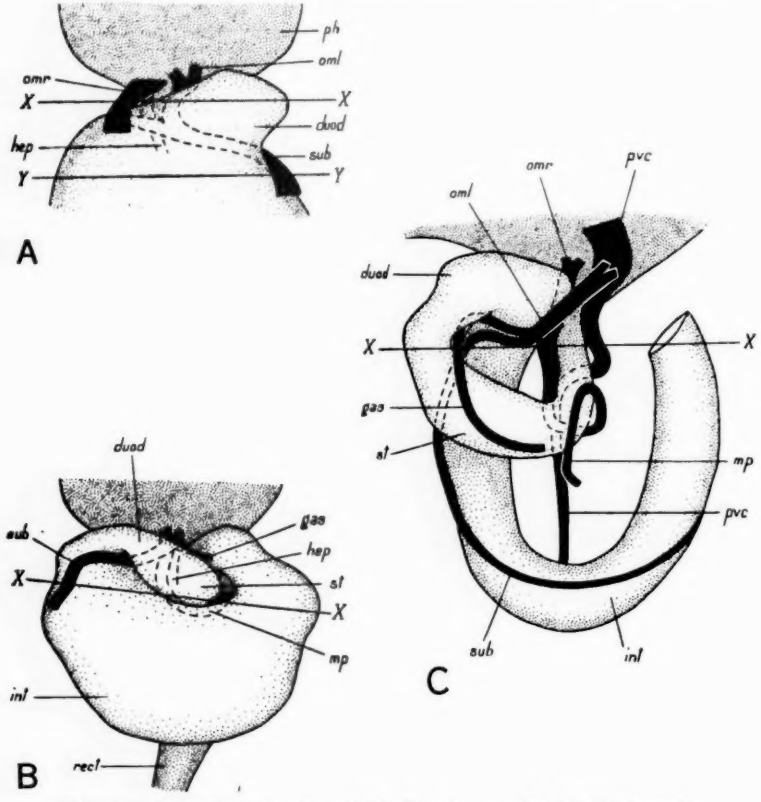
The first veins to be laid down in the embryo are the omphalomesenterics. These appear in 4 mm. embryos. They lie along the ventro-lateral sides of the yolk-laden gut, and open into the heart.

In 6 mm. embryos the liver is present as a ventral diverticulum of the gut. The heart lies anterior to this diverticulum, and the omphalomesenterics run along the ventro-lateral edges of it and open into the ducts of Cuvier (see Plate V, fig. 1). Opening into the left omphalomesenteric is a short vein from the dorso-lateral edge of the liver diverticulum, the beginning of a dorsal anastomosis round the gut (see Plate V, fig. 2, *anast*).

At 6·5 mm. the left omphalomesenteric has lost its connexion with the heart and breaks up into a rete mirabile in the developing liver. This left omphalomesenteric is much longer than the right, and may now be known as the subintestinal vein. With the completion of the dorsal connexion round the gut, the ventral connexion has broken down and the course of the vein is now as follows (text-fig. 1A): it commences on the left side of the posterior gut (Plate V, fig. 4), crosses the future duodenal region dorsally and passes through the *anlage* of the pancreas at the left omphalomesenteric. The right omphalomesenteric still opens into the heart. There is an anastomosis between the right omphalomesenteric and the subintestinal vein dorsal to the liver diverticulum. The hepatic vein has appeared as an independent formation leading from the dorsal portion of the liver into the right duct of Cuvier posterior to the entry of the right omphalomesenteric (see Plate V, fig. 3). (It is thus an independent structure and not formed from either omphalomesenteric.) In addition to the hepatic vein numerous small sinusoids from the liver open directly into the sinus venosus. Later these are all gathered together into the hepatic vein.

The right omphalomesenteric vein loses its connexion with the heart in 7 mm. larvae. Throughout, the two omphalomesenterics maintain their position along the ventral surface of the liver, one on either side of the bile duct (the original connexion between the gut and the liver diverticulum)

(see Plate VI, fig. 1). There are usually one or two anastomoses between the right omphalomesenteric and the subintestinal (or left omphalomesenteric)



TEXT-FIGURE 1.—Reconstructions of the alimentary canal and its blood-vessels. A. 6·5 mm. tadpole, × 45 (X–X marks position of section in Plate V, fig. 3, and Y–Y in Plate V, fig. 4). B. 8 mm. tadpole, × 45 (X–X marks position of section in Plate VI, fig. 3). C. 24 mm. tadpole, × 19 (X–X marks position of section in Plate VII, fig. 2). All in ventral view. In C the posterior portion of the intestine is removed. For abbreviations see p. 99.

dorsal to the bile duct. The posterior part of the subintestinal has now a mid-ventral position (Plate VI, fig. 2).

In 8 mm. larvae the coiling of the gut has commenced (text-fig. 1, B). The stomach is distinct (identified by the presence of the gastric glands), the duodenum has an anterior loop on the right side of the body, and the

ileum has an anterior loop on the left side of the body. As a result the subintestinal vein has been carried over to the right side with the duodenum (Plate VI, fig. 3). It still runs through the pancreas and crosses the duodenum dorsally. It has also acquired a gastric branch from the stomach, which joins it in the anterior region of the pancreas. A new vein (*mp*) has come to open into the right omphalomesenteric (Plate VI, fig. 3; text-fig. 1, B). It comes from the region of the ileum (and later from the spleen as well), passes forwards in the dorsal mesentery ventral to the postcardinal veins, crosses the posterior vena cava (when developed) ventrally to the right side, passes on to the ventral surface of the right part of the liver and joins the right omphalomesenteric.

These conditions persist more or less up to the time of metamorphosis (text-fig. 1, C; Plate VII, fig. 2). Vein *mp* becomes better developed with the complicated coiling of the ileum. The subintestinal drains the ventral surface of the first limb of the ileum, the duodenum and the pancreas. There is usually at least one anastomosis between the right and left omphalomesenterics in the region of the liver dorsal to the bile duct.

At metamorphosis great changes in appearance and position are brought about by the shrinkage and shortening of the gut. The vein *mp* of the larva still drains the spleen and the posterior part of the gut; it becomes the main portal vein of the adult and opens into the right lobe of the liver (on the right side of the bile duct). It also receives the anterior gastric vein from the anterior dorsal surface of the stomach.

The subintestinal vein of the larva becomes the gastro-duodenal of the adult. It drains the pancreas, ventral duodenum and stomach, and opens into the left lobe of the liver. Its branch, the gastric, becomes the median gastric of the adult.

The original anastomosis between the omphalomesenteric veins persists as the connexion between the main portal and the gastro-duodenal.

The abdominal vein at metamorphosis becomes connected with the gastro-duodenal vein (subintestinal of larva) at approximately its junction with the median gastric.

The development of the system may be summarised as follows (see text-fig. 2):

Stage 1. Two omphalomesenterics open into heart. (4 to 5 mm.)

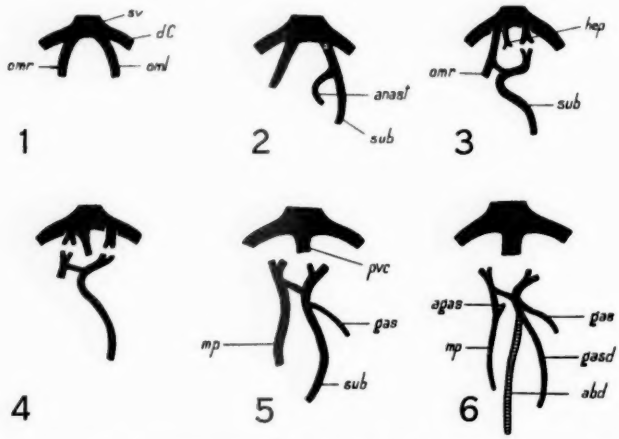
Stage 2. Left omphalomesenteric becomes subintestinal vein. (6 mm.)

Stage 3. Left omphalomesenteric loses connexion with heart. Hepatic vein appears independently of omphalomesenterics. Subintestinal lengthens. (6·5 mm.)

Stage 4. Right omphalomesenteric loses connexion with heart. (7 mm.)

Stage 5. Main portal vein opens into right omphalomesenteric. Subintestinal with gastric and gastro-duodenal branches. (8 mm. to metamorphosis.)

Stage 6. Alterations in length and position of above veins. Abdominal vein joins subintestinal. (Metamorphosis.)



TEXT-FIGURE 2.—A diagrammatic representation of the development of the omphalomesenteric veins and hepatic portal system in ventral view (not to scale). Stage 1: 5 mm. tadpole; stage 2: 6 mm.; stage 3: 6·5 mm.; stage 4: 7 mm.; stage 5: 8–40 mm.; stage 6: metamorphosis. For abbreviations see p. 99.

DISCUSSION.

1. *Persistence of Right Omphalomesenteric Vein.*

Xenopus differs from other Salientia so far described in the fact that the afferent part of the right omphalomesenteric vein persists throughout life, and receives the main branch of the hepatic portal system.

In Salientia, according to Hochstetter (1888 and 1906), both omphalomesenterics break up into venous networks in the liver, forming afferent and efferent portions. The afferent portion of the right vein atrophies, that of the left receives the hepatic portal vein.

A resemblance to the condition in *Xenopus* is perhaps to be found in the development of *Salamandra* (Choronshitzky, 1900, quoted by Hochstetter, 1906 (footnote, p. 124), and Kerr, 1919). Here the mesenteric vein opens first into the right omphalomesenteric, but later, on the atrophy of the latter vein, into the left omphalomesenteric.

Weisz (1945, *a* and *b*) mentions an intestinal vein which opens into the mesonephric sinus in *Xenopus* tadpoles. The writer was unable to discover any such vein, and it can only be thought that Weisz had found the main portal vein (vein *mp*) but was unable to trace it to its junction with the right omphalomesenteric. This mistake can be understood since the vein crosses exceedingly close to the origin of the posterior vena cava from the mesonephric sinus.

A point of interest which might be noted here is that the vein of the adult which is commonly known as the ramus dexter of the vena abdominalis is shown by the ontogeny not to be part of the abdominal vein at all, but the original embryonic connexion between the right and left omphalomesenteric veins. The abdominal vein acquires connexion with the left omphalomesenteric vein only (*cp.* text-fig 2). Similar conclusions have been reached by O'Donoghue (1931) on the development in *Rana*.

The latter fact satisfactorily accounts for several of the common adult variations (Millard, 1942), namely:

(*a*) The so-called ramus dexter of the abdominal vein is often absent in the adult. A corresponding variation is found in the larval stages. Most commonly there is one anastomosis between right and left omphalomesenterics, but often there are two (of which one apparently atrophies later), and sometimes none at all.

(*b*) In the adult the median gastric and gastro-duodenal branches may join before entering the so-called ramus sinister of the abdominal, or (more commonly) enter it separately. The condition depends simply on whether the abdominal acquires its connexion with the subintestinal anterior or posterior to the junction of the median gastric.

2. *Persistence of Subintestinal Vein.*

In the development of the Urodeles a subintestinal vein is present on the mid-ventral surface of the gut. It is formed by the fusion of the posterior ends of the two omphalomesenterics, and on the disappearance of the anterior part of the right omphalomesenteric remains connected with the left. This vein is considered by Hochstetter (1888) to be homologous with the subintestinal of fishes, which also is formed by the fusion of two omphalomesenterics, only in Urodeles it is never connected with the caudal. After the development of the true hepatic portal vein (dorsal to the gut) the persisting part of the subintestinal is known as Rusconi's vein. It has also been identified by Kimball (1928) in various reptile and bird embryos and in *Didelphys*.

In the Salientia, according to Mollier (1906), Rusconi's vein is not

present and the omphalomesenterics are lateral in position. In *Xenopus*, however, a vein is present, which, although it is formed from only one omphalomesenteric, the author feels justified in calling the subintestinal. Its position and course are similar to those of the vein described by Hochstetter (1906), van Gelderen (1933) and Kimball (1928). It commences on the ventral surface of the anterior part of the small intestine, crosses the duodenum dorsally and joins the left omphalomesenteric in the region of the liver (text-fig. 1).

This vein (although relatively shorter in length) persists to form part of the hepatic portal system of the adult (the gastro-duodenal vein), which portion might well be termed Rusconi's vein. Such a maintenance of the subintestinal is considered by Hochstetter to be a primitive condition.

3. *Origin of Hepatic Vein.*

Xenopus differs from all other Amphibia in that the hepatic vein, when first laid down, is not formed from the omphalomesenterics, but is an independent structure opening directly into the right duct of Cuvier. Later it becomes more median in position. It follows that the anterior portion of the posterior vena cava, which is formed by the hepatic vein, cannot be homologised with the omphalomesenterics. It is possible, though difficult to determine with certainty, that as the hepatic vein enlarges the efferent portions of the omphalomesenterics become incorporated in it.

Development of the Posterior Blood Vessels.

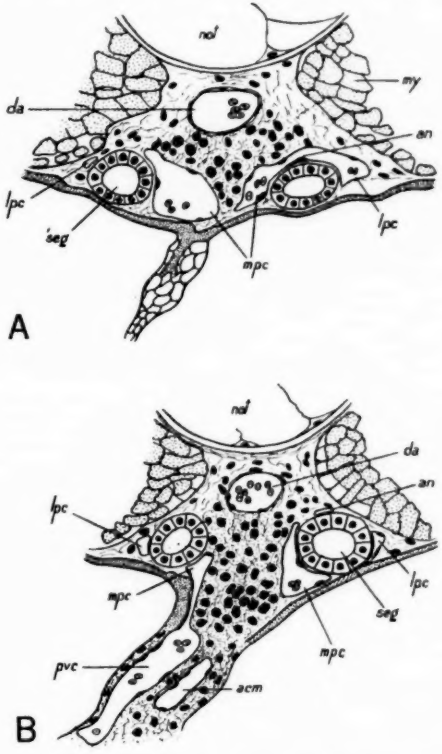
1. *The Postcardinals and Renal Portal Veins.*

Anterior and posterior cardinal veins are present in 5 mm. embryos. Both open into a sinus amongst and partially surrounding the pronephric tubules. From this pronephric sinus the duct of Cuvier runs diagonally forwards and inwards to the heart.

In later embryos (6 to 6·5 mm.) each postcardinal vein extends posteriorly from the pronephric sinus along the medial side of the Wolffian duct. Posterior to the opening of the cloaca it joins the one from the other side to form a median caudal vein (text-fig. 5, A). The caudal vein lies ventral to the caudal gut and corresponds to the posterior end of the subintestinal vein of fishes (Hochstetter, 1888).

As development proceeds the point of junction of the postcardinals gradually moves forwards. In 7 to 9 mm. tadpoles (where the caudal gut has disappeared) the two postcardinals join at a point between the opening of the cloaca and the openings of the Wolffian ducts into the cloaca, but

are also connected with each other by anastomoses anterior to the latter point (see Plate I, and text-fig. 5, B). In 10 mm. tadpoles the postcardinals join anterior to the openings of the Wolffian ducts, but are again connected

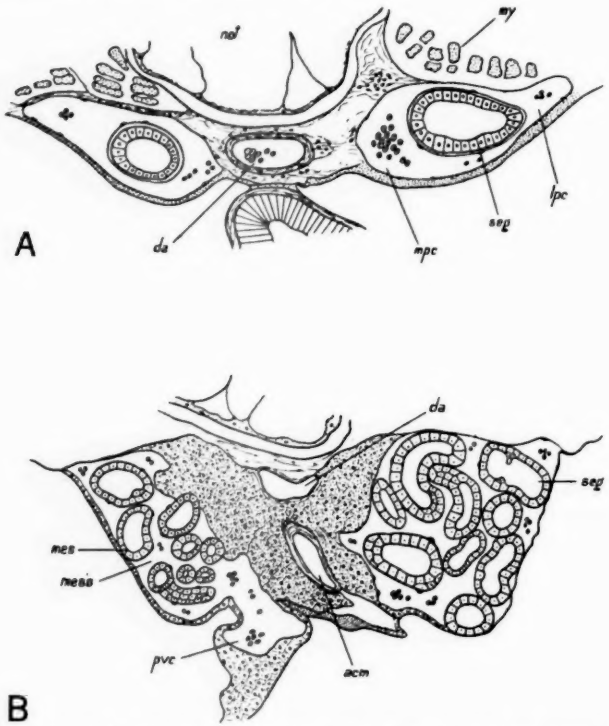


TEXT-FIGURE 3.—Sections through a 10 mm. tadpole showing the relations of the postcardinal veins to the Wolffian ducts. Both sections pass through the region where the median postcardinals are unfused. In A the lateral postcardinals (*lpc*) consist of isolated portions of vessels. B is more anterior and passes through the junction of the posterior vena cava (*pvc*) with the right median postcardinal (*mpc*). The lateral postcardinals are here continuous. × 250. For further abbreviations see p. 99.

by anastomoses more anteriorly (text-fig. 5, C). In 12 mm. tadpoles the postcardinal veins join just posterior to the junction of the posterior vena cava with the right postcardinal. Anterior to this point they remain separate (text-fig. 5, D).

These vessels are the median postcardinals of Engels (1935) and others,

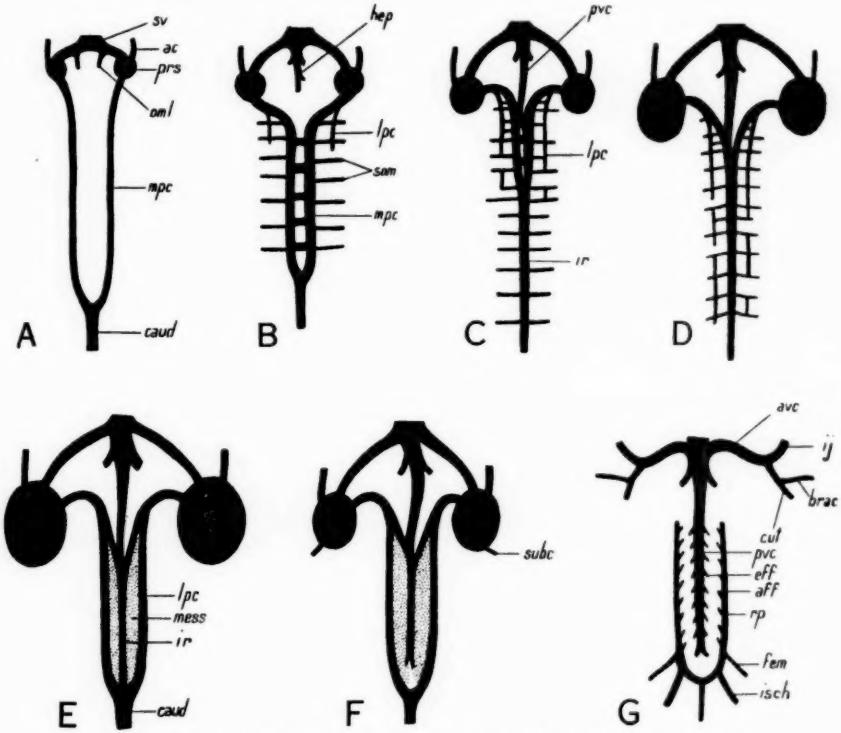
and are situated median to the Wolffian ducts (Plate VI, fig. 2; text-fig. 3). By their fusion they form the interrenal vein (vena cardinalis impar of Engels, subcardinal of van Gelderen, 1933) which lies in the mid-line between the *anlagen* of the mesonephroi (Plate II).



TEXT-FIGURE 4.—Sections through a 24 mm. tadpole showing the relations of the postcardinal veins. In A each Wolffian duct (*seg*) is completely surrounded by a blood sinus formed by the fusion of the median and lateral postcardinals (*mpc* and *lpc*). B is more posterior and passes through the mesonephros at the point where the posterior vena cava (*pvc*) joins the mesonephric sinus (*mess*). × 110.

During the period in which the median postcardinals fuse in the mid-line, the lateral postcardinals (Jacobson's veins) make their appearance. They are first recognisable in 8 mm. tadpoles as narrow vessels extending for a very short distance posteriorly from the pronephric sinuses lateral to the Wolffian ducts. They are connected with the median postcardinals by a number of anastomoses passing dorsal and ventral to the Wolffian ducts

(text-fig. 3; Plate I). Laterally they receive somatic vessels from the myotomes. More posteriorly these lateral postcardinals are represented by isolated portions of vessels lateral to the Wolffian ducts and connected with the median postcardinals by anastomoses. It is difficult to determine



TEXT-FIGURE 5.—A diagrammatic representation of the development of the postcardinal veins and posterior vena cava in ventral view (not to scale). A. 6 mm. tadpole; B. 8 mm.; C. 10 mm.; D. 12 mm.; E. 14 mm.; F. 24 mm.; G. Metamorphosis. For abbreviations see p. 99.

whether these isolated portions develop from lateral outgrowths from the median postcardinals, or from anterior and posterior outgrowths from the somatic vessels.

In the ensuing stages the lateral postcardinals continue to develop in an anterior-posterior direction, until in 14 mm. tadpoles they are continuous vessels extending from the pronephric sinuses to the region where the Wolffian ducts open into the cloaca, where they finally join the interrenal

vein (text-fig. 5, E). At the same time the dorsal and ventral anastomoses with the median postcardinals increase in width and fuse with one another. In this way there is formed on each side in the anterior region (where the median postcardinals are unfused) a continuous sinus surrounding the Wolffian duct (text-fig. 4, A). Of this sinus the median portion is formed by the median postcardinal, and the lateral portion by the lateral postcardinal. Further back (in the region where the median postcardinals have fused to form the interrenal) a network of vessels is formed on each side amongst the developing mesonephric tubules and connecting the lateral postcardinal with the interrenal vein. This system of vessels gradually assumes the form of a complete sinus surrounding the mesonephric tubules, of which the main central channel is formed by the interrenal vein (or interrenal part of the posterior vena cava), and the main lateral channel by the lateral postcardinal (text-fig. 4, B; Plate II). As they pass backward the lateral postcardinals gradually become more distinct from the rest of the system. At a later stage the interrenal vein loses its direct connexion with the caudal in the posterior region of the kidneys. This condition persists up to the time of metamorphosis.

During metamorphosis the sinus surrounding the mesonephroi assumes the form of a vascular network (rete mirabile), and the lateral postcardinals (Jacobson's veins) and the posterior vena cava remain connected with it by afferent and efferent renal vessels respectively (Plate III; text-fig. 5). The pronephroi disappear completely, together with the anterior portions of the Wolffian ducts. With them go the pronephric sinuses and the paired portions of the median postcardinals (*i.e.* those portions which, together with the anterior ends of the lateral postcardinals, surround the pronephric ducts). In this way, since the posterior vena cava has already become disconnected from the caudal vein, the renal portal system loses any direct communication with the posterior vena cava. The femoral and ischiadic veins from the hind limbs open into Jacobson's veins, and with the disappearance of the tail the caudal vein and its connexions with Jacobson's veins disappear.

2. *The Posterior Vena Cava.*

The posterior vena cava is present as such for the first time in 9 mm. tadpoles. It lies along the dorsal surface of the liver and joins the right median postcardinal vein in the region where the coeliaco-mesenteric artery is given off by the dorsal aorta. It is formed by the growth of the hepatic vein through the liver in a posterior direction (text-fig. 3, B, and 4, B). At first this hepatic vein is surrounded by liver tissue almost entirely to the point where it joins the postcardinal. Later the posterior liver tissue shrinks away, leaving an independent posterior vena cava.

Gradually the posterior vena cava takes over the main blood stream from the interrenal, and thus the interrenal and a small portion of the right median postcardinal come to form the posterior part of the posterior vena cava. Up to 14 mm. this composite posterior vena cava is directly continuous with the caudal vein, but after this the connexion is broken in the posterior region of the mesonephroi (text-fig. 5; Plates I to III).

3. *Discussion.*

The earlier accounts of the development of the postcardinal and renal portal systems in the Salientia are those of Hochstetter (1888) in various genera, Gaupp (1896) in *Rana esculenta*, and Shore (1902) in *Rana* sp. More recent accounts include those of Kampmeier (1920) in *Bufo vulgaris* and *B. lentiginosus*, and Engels (1935) in *Rana fusca*.

The first stages of development apparently run parallel in *Xenopus* and other Salientia and the early postcardinals and posterior vena cava have a similar position and course. In all cases the postcardinals fuse in the midline to form an interrenal vein which eventually forms part of the posterior vena cava.

As regards the manner of formation of the renal portal system in the Salientia there seems to be some difference of opinion. According to Goette (quoted by Hochstetter), Hochstetter, Gaupp and Kampmeier the lateral postcardinal develops as a longitudinal anastomosis between the somatic veins lateral to the Wolffian duct.

According to Shore the first-formed postcardinals come to surround the Wolffian ducts at an early stage, so that when the mesonephroi develop "the nephridial cylinders have begun to grow into the cardinal veins, which are beginning to be broken up into a network of venous sinuses closely surrounding the cylinders, similar to the condition around the pronephros". In this manner a system of sinuses is formed surrounding the mesonephroi, with a well-marked "median mesonephric channel" (*i.e.* interrenal vein) and "lateral mesonephric channels" (*i.e.* lateral postcardinals).

Engels describes a similar system of sinuses, but according to his account the lateral postcardinal is formed by the fusion of a number of so-called blood-islands lateral to the Wolffian duct, which have apparently grown out from the median postcardinal. This description agrees most closely with that described above for *Xenopus*.

However the future Jacobson's vein is formed, whether by a longitudinal anastomosis between the somatic vessels, or by the growth of the median postcardinal around the Wolffian duct, or by the fusion of isolated portions of blood-vessels, it undoubtedly belongs to the cardinal system and can rightly be called a lateral postcardinal. This brings the Salientia into line

with the rest of the Vertebrate series, where the renal portal (Jacobson's) vein is always formed in some manner from the postcardinal veins:

(*a*) In Selachians the renal portal vein is the direct continuation of the lateral postcardinal, but has become secondarily detached from the postcardinal and connected with the caudal vein (van Gelderen, 1933, and Hochstetter, 1906).

(*b*) In the Dipnoi (*Lepidosiren*) the median and lateral postcardinals are formed by the fusion of series of blood-spaces situated respectively median and lateral to the pronephric duct. The lateral postcardinals maintain their connexions with the caudal vein and form the renal portals (Robertson, 1913).

(*c*) In *Salamandra atra* the postcardinals at first surround the pronephric ducts, then split longitudinally, of which the inner portions unite to form the mesonephric part of the posterior vena cava, while the outer portions form the renal portals (Hochstetter, 1888 and 1906).

(*d*) In reptiles (*Lacerta*) the original postcardinals become resolved into external and internal components, of which the external connect with the caudal vein to form a renal portal system (Hochstetter, 1892, quoted by Kerr, 1919).

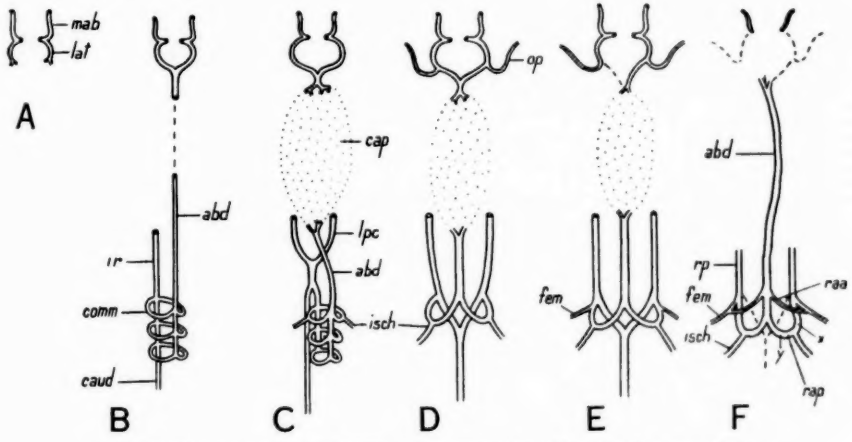
These differences in the manner of formation of the renal portal or Jacobson's veins in the Vertebrate series are undoubtedly due to the process of "heterochrony" in which, according to de Beer (1940), the order in which characters appeared in a previous ontogeny is not always faithfully reproduced in the ontogeny of the descendants.

Development of the Abdominal and Hind Limb Veins.

The abdominal vein of the adult develops from two lateral veins, which are present for the first time in 6·5 mm. larvae; they drain the ventral body-wall and open into the sinus venosus together with the muscularis abdominis veins. (See Plate I, and Plate VI, fig. 1.)

During development the lateral veins grow backward and join in the mid-ventral line to form a median vessel, which collects blood from a network of capillary vessels on the ventral body-wall. This capillary network is also drained by another median vessel in the posterior region. This second vein passes backward along the ventral body-wall and connects with the caudal vein by a number of irregularly arranged commissural vessels encircling the cloaca and receiving small branches from it. In one larva only (10 mm.) were the anterior and posterior median vessels (portions of the future abdominal vein) continuous throughout the length of the abdomen (text-fig. 6, B).

In 24 mm. tadpoles the hind limb-buds are developing and the ischiadic veins are present and open into one of the posterior commissural vessels (Plate II, B; text-fig. 6, C). This particular commissural vessel (usually the most anterior one) persists during development and maintains a connexion between the abdominal vein and the renal portal system, while the others disappear. Moreover, with the further development of the mesonephroi, the lateral postcardinals are lengthened by a longitudinal splitting of the caudal vein, so that each commissural vessel with its ischiadic branch comes to open into the lateral postcardinal or renal portal vein (text-fig. 6, D).



TEXT-FIGURE 6.—A diagrammatic representation of the development of the abdominal and hind limb veins in ventral view (not to scale). A. 7 mm. tadpole; B. 10 mm.; C. 18–24 mm.; D. 37 mm.; E. Early metamorphosis; F. Adult. Note that in C the ventral part of the caudal vein receiving the commissural vessels has been longitudinally split off from the dorsal part. For abbreviations see p. 99.

The femoral vein appears later (44 mm. tadpoles), and opens into the commissural vessel between the connexion of the latter with the renal portal and the junction of the ischiadic vein (text-fig. 6, E; Plate III). At metamorphosis the caudal vein and the portions of the renal portals posterior to the junction of the commissural vessel disappear. Each femoral vein acquires an independent connexion with the median ventral or abdominal vein. This connexion becomes the anterior anastomosis or ramus abdominalis anterior of the adult. Hence it is evident that the original commissural vessel gives rise to the following portions of the adult system: (*a*) the proximal portion of the ischiadic vein and a small part of the adult renal

portal vein (*x*, text-fig. 6, F), and (*b*) the posterior anastomosis or ramus abdominalis posterior of the adult (*y*, text-fig. 6, F).

During the later developmental stages changes also occur in the lateral veins or anterior part of the system. In 37 mm. tadpoles the lateral veins * not only drain the capillary network on the ventral body-wall, but receive a pair of veins from the opercula (text-fig. 6, D, *op*). In an early stage of metamorphosis the right lateral vein is absent posterior to the junction of the opercular vein (text-fig. 6, E; Plate III). The change from this stage to the adult condition, which is found in the later stages of metamorphosis, apparently occurs very rapidly, and no further intermediate stages could be found. In the adult the abdominal vein is continuous along the ventral body-wall and has acquired a connexion with the hepatic portal system. The left lateral vein and both opercular veins have vanished.

Discussion.

As far as the writer is aware only two descriptions exist of the development of the abdominal vein in the Amphibia. The first is by Goette (1875) in *Bombinator igneus* (subsequently quoted by Gaupp, 1896, and Hochstetter, 1888 and 1906), and the second by Hochstetter (1894) in *Salamandra maculata*.

Hochstetter (1888) considers that the abdominal vein of Amphibia is homologous with the paired lateral veins of Selachians, a conclusion that is supported by the ontogeny of *Xenopus*. The homology is based on the following facts:—

(*a*) The abdominal vein in the Amphibia develops from paired rudiments, which during the early stages enter the heart. This is the state of affairs in *Bombinator* and in *Xenopus*, but in *Salamandra* the anterior portion of the right vein is absent. The connexion with the hepatic portal system is secondary and established only at metamorphosis.

(*b*) The position of the veins is similar in Amphibia and in Selachians, namely, in the ventrolateral region of the body-wall. In the Amphibia, however, the veins later fuse in the mid-line. In *Xenopus* the posterior part of the vein is single throughout development.

(*c*) The drainage area of the abdominal vein is similar to that of the lateral veins, *i.e.* the ventral body-wall itself, the cloaca (and the bladder in Amphibia) and the hind limbs or fins.

* These veins could not always be traced back as far as their junction in the mid-ventral line.

In older tadpoles of *Xenopus* the abdominal vein is represented by (*a*) an anterior median vessel formed by the junction of the lateral veins, and (*b*) a posterior vessel draining into the renal portal system, the two being separated by a venous network on the ventral body-wall (text-fig. 6). This arrangement as seen in sectioned material indicated that blood flows forward in the anterior vessel and backward in the posterior one. This was confirmed by examination of anaesthetised tadpoles under a high-power dissecting microscope. At metamorphosis, when the abdominal vein becomes continuous, there must consequently be a change in the direction of flow in the posterior vessel. A similar change in the direction of flow is described by Hochstetter (1894) in *Salamandra*.

From the development of *Xenopus* it is evident that the ischiadic vein is not a posterior continuation of the lateral vein, nor of the renal portal vein. It is a vein developed as a drainage system for the hind limb-bud, which apparently simply enters the vessel nearest in position. This happens to be one of the commissural vessels between the abdominal and caudal veins.

The arrangement of the hind limb veins in *Pipa* almost exactly resembles the stage depicted in text-fig. 6, E, of a metamorphosing specimen of *Xenopus*, except of course that the caudal vein has disappeared. The diagram given by Grönberg and Klinckowström (1893) suggests a similar development in *Pipa*, namely, that the femoral and ischiadic veins arise as tributaries of an anastomosis between the abdominal vein and the renal portal.

This condition of the hind limb veins in the Pipidae is interesting, in that it provides an intermediate stage between that of Selachians, where the veins from the pelvic fins open into the lateral abdominal veins, and that found in the Ranid type of Salientian, where the iliac veins open into the mesonephric sinuses in young stages.

O'Donoghue (1931) has summarised the existing accounts, and described a number of new examples of persistent lateral abdominal veins in the frog. Most of these accounts apply to *Hyla aurea* and *Rana spp.*, and one account to *Bufo melanostictus*. In most of the examples the posterior portion of the abdominal vein is median and single. In two examples, however (*Hyla aurea* and *Rana temporaria*), the persistent lateral abdominal veins are paired throughout. This possibly indicates that the course of development in the Ranidae and Hylidae is different from that of *Xenopus*, since at no time in the development of *Xenopus* are there paired vessels in the posterior abdominal region.

Conditions in abnormal cases of *Rana* and *Hyla* lead O'Donoghue to the conclusion that the anterior portion of the left lateral vein must disappear before that of the right. In *Xenopus*, in the stage of early metamorphosis studied, the posterior portion of the right vein had disappeared before that

of the left. Events happen so rapidly at metamorphosis, however, that the interval of time between the disappearance of right and left veins is necessarily very short, and it is considered by the writer to be a matter of small importance which vein disappears first.

The only relevant abnormalities found in *Xenopus* were two specimens with looped abdominal veins. In one the looping was in the anterior region, in the other in the posterior region. Bearing in mind the vascular network on the ventral surface during the young stages, this looping is not considered to be particularly significant, and is certainly not pronounced enough to indicate paired abdominal veins in the posterior region.

Development of the Veins of the Lower Jaw and Ventral Branchial Region.

In this description of the veins of the ventral region of the head, the same names are used as in the description of the adult (Millard, 1941) although the embryology shows that they are not particularly appropriate. The homologies of the vessels are discussed at the end of the chapter.

1. *The External Jugular Veins.*

The external jugular is the main vein responsible for the drainage of the branchial arches and filter apparatus throughout the larval stages. It is first present in 6·5 mm. larvae and enters the duct of Cuvier dorsal to the vena muscularis abdominis. Its course has already been described and figured by Paterson (1939 and 1942) and by Weisz (1945, *a* and *b*), although wrongly called the internal jugular by the latter. It passes along the mediodorsal edge of the branchial basket, ventral to the columnar epithelium of the pharynx (or "pharyngo-branchial tract" of Weisz); passes lateral to the larynx and laryngeal muscles, crosses the aortic arches dorsally, and finally turns ventrally to join the duct of Cuvier (see Plate VII, fig. 1). During its course it drains the floor of the pharynx, musculus subarcualis rectus i and the thyroid gland, and also receives the following branches from the branchial basket, each of which is situated slightly dorsal to the corresponding branchial artery (Plate II; Plate VII, fig. 1);

(*a*) A branch from the filter apparatus of branchial arches 1 and 2, with a small subsidiary branch from the columnar epithelium of branchial arch 2.

(*b*) A branch from the filter apparatus of branchial arch 3, with a subsidiary branch from the columnar epithelium of this arch.

(*c*) A branch from the filter apparatus of branchial arch 4 (not mentioned by Paterson), entering the external jugular immediately before it joins the duct of Cuvier.

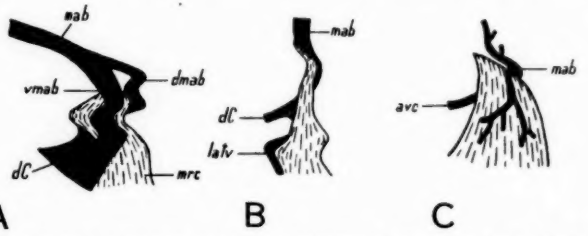
After metamorphosis and the disappearance of the branchial basket the external jugular loses its branchial branches but remains to drain the hyoid apparatus, the pharynx, and the surrounding structures. It is situated between the pharynx and the hyoid cartilage.

2. *The Musculo-thyroid Veins.*

The musculo-thyroid vein is not present during the larval stages. It is first visible in sections of a young frog immediately after the completion of metamorphosis, where it runs along the ventral surface of the larynx, crossing the attachment of musculus petrohyoideus ventrally and the aortic arches dorsally to join the anterior vena cava proximal to the vena jugularis externa. At this stage the right and left vessels are approximately equal in size, the typical asymmetry only becoming evident later. The two vessels fuse anteriorly in the mid-line. Later in development the musculo-thyroid anastomoses at several points with the external jugular and takes over some of the work of the latter, namely, the drainage of the thyroid gland and the muscles attached to the hyoid apparatus.

3. *The Muscular Abdominal Veins.*

Throughout the younger stages of development the ventral part of the head region is drained chiefly by a pair of stout veins which give rise to the



TEXT-FIGURE 7.—Diagram to show the relations of vena muscularis abdominis (*mab*) and v. lateralis (*latv*) to the rectus cervicis muscle (*mrc*). All in ventral view. A. Reconstruction of 6 mm. tadpole, × 109. B. Reconstruction of tadpole during early stages of metamorphosis, × 11. C. Adult frog (diagrammatic). For further abbreviations see p. 99.

muscular abdominal veins of the adult (hypobranchial veins of Weisz, 1945, and 1945 *a*). These veins are seen for the first time in 6 mm. larvae and their course is as follows (see text-fig. 7, A): in the anterior region each vein is situated medial to the ventral edge of the lateral plate mesoderm, it passes posteriorly crossing the aortic arches ventrally to enter the duct of Cuvier by two roots. The better developed of the two roots crosses the musculus

rectus cervicis medially and ventrally, and the other root crosses dorsally and laterally. In 6·5 mm. and older tadpoles the course is similar, except that only the dorsal root is present, and this dorsal root enters the duct of Cuvier together with the lateral vein, which is now visible (text-fig. 7, B). The vein is exceedingly well developed throughout the larval stages, even after the full development of the vena jugularis externa, and its course in the larger tadpoles is as follows (Plates I to III; Plate VII, fig. 1): it is situated throughout its course on the ventral surface of the branchial basket, crossing the musculus interhyoideus, the m. transversus ventralis ii, and the aortic arches ventrally. In the region of the m. rectus cervicis it passes on to the ventral surface of the muscle, then passes round its lateral edge on to the dorsal surface, and enters the sinus venosus together with the lateral vein. It drains m. intermandibularis, m. quadrato-hyo-angularis, m. interhyoideus, m. orbitohyoideus, the lateral wall of the pharynx (in the anterior region), ventral skin (in anterior region), m. geniohyoideus, and mm. subarcuales recti iii and iv.

After metamorphosis the vein decreases considerably in importance, the greater part of its work apparently being taken over by the external jugular and musculo-thyroid veins. It persists as a relatively small vein, the v. muscularis abdominis, which commences on the ventral surface of the m. rectus cervicis and passes round its lateral edge to enter the heart (see text-fig. 7, C). In the adult it drains the muscles of the ventral body-wall (mm. rectus abdominis and sternohyoideus) in a more restricted region. It may then have a secondary anastomosis with the abdominal vein on the ventral surface of these muscles.

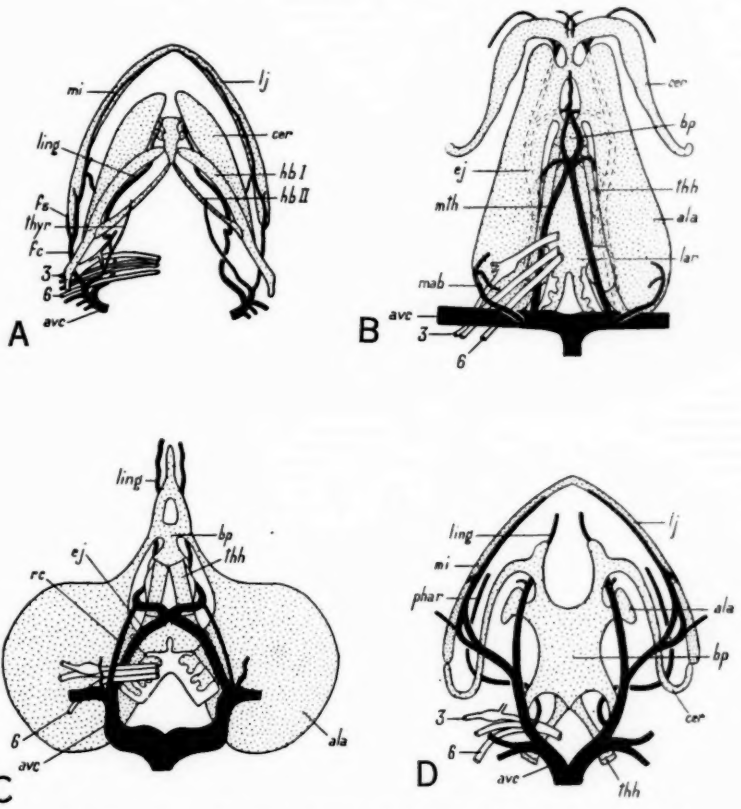
4. *Discussion.*

The homologies of the external jugular veins are a matter of great difficulty on account of the considerable amount of variation found among the various members of the Amphibia. It is considered by the writer that the three veins described above, namely, the external jugular, the musculo-thyroid and the muscularis-abdominis, all represent elements of the external jugular. The fundamental plan is more comprehensible when compared with a primitive type such as *Salamandra* than when compared with a specialised type such as *Rana*.

In *Salamandra*, as described by Francis (1934), the external jugular consists of three elements (text-fig. 8, A), namely:

(i) *A dorsal element, or v. lingualis*, draining the tongue, m. subarcualis rectus i and ventral pharyngeal wall, and crossing the branchial skeleton and aortic arches dorsally.

(ii) *A ventral element, or v. thyroidea*, draining the thyroid gland and the ventral skin, and crossing the branchial skeleton and aortic arches ventrally.



TEXT-FIGURE 8.—Diagrams showing the relations of the elements of the external jugular veins in A. *Salamandra salamandra* (summarised from Francis, 1934); B. *Xenopus laevis*; C. *Pipa americana* (summarised from Grönberg and Klinckowström, 1893); and D. *Rana esculenta* (summarised from Gaupp, 1896). All in ventral view. The right aortic arches have been shown in position in each case. For abbreviations see p. 99.

(iii) *A ventrolateral element, or v. facialis communis*, receiving vessels from the orbit, the superficial intermandibular region, the thymus and skin, and crossing the aortic arches ventrally.

These three elements are considered to be respectively homologous with the vena jugularis externa, vena muscularis-thyroidea and vena muscularis abdominis of *Xenopus*, although the latter receives no component from the facial region.* The homologies cannot be based on the drainage of the vessels, since this varies considerably, nor on the position relative to the aortic arches, since the vessels may fuse with one another at varying points (*i.e.* either anterior or posterior to the aortic arches), but on the general position of the vessels in the body, particularly in relation to the hyoid skeleton. The dorsal element is always dorsal and the ventral element ventral to the hyoid and branchial skeletons. The ventrolateral element is always situated on the lateral region of the lower jaw in adult stages and crosses the aortic arches ventrally.

Bearing these points in mind it is possible to draw up the following table summarising the elements of the external jugular veins in those Amphibia of which sufficiently detailed descriptions exist, namely *Salamandra salamandra* (Francis, 1934), *Xenopus laevis* (Millard, 1941), *Pipa americana* (Grönberg and Klinckowström, 1893), and *Rana esculenta* (Gaupp, 1896). See also text-fig. 8.

	Dorsal Element	Ventral Element	Ventrolateral Element
Salamandra	v. lingualis	v. thyroidea	v. facialis communis
Xenopus	v. jugularis externa	v. muscularis-thyroidea	v. muscularis abdominis
Pipa	v. lingualis	v. jugularis externa	ramus communicans?
Rana	v. pharyngea	v. lingualis	v. mandibularis interna.

The three elements of the external jugular in Amphibia in general may be summarised as follows:

(i) *The dorsal element.* Known as the v. lingualis in *Salamandra* and *Pipa*, the v. jugularis externa in *Xenopus*, and the v. pharyngea in *Rana*. Situated dorsal to the hyoid and branchial skeleton and

* This corrects a statement made in a previous paper (Millard, 1941) that the element corresponding to the v. facialis communis is absent in *Xenopus*.

draining chiefly the mucous membrane of the pharynx. May also receive branches from the larynx, tongue, thyroid glands and various muscles. May join the v. cava anterior separately as in *Xenopus* and *Salamandra* or may be a branch of the ventrolateral element as in *Pipa* and *Rana*.

(ii) *The ventral element.* Known as the v. thyroidea in *Salamandra*, the v. muscularis-thyroidea in *Xenopus*, the v. jugularis externa in *Pipa* and the v. lingualis in *Rana*. Situated ventral to the hyoid and branchial skeleton and draining chiefly the thyroid gland. May also receive branches from the larynx, mucous membrane of the pharynx, and the tongue. May cross the aortic arches ventrally, as in *Salamandra* and *Rana*, or dorsally, as in *Xenopus* and *Pipa*.

(iii) *The ventrolateral element.* Known as the v. facialis communis in *Salamandra*, the v. muscularis abdominis in *Xenopus* and the v. mandibularis interna in *Rana*. Situated in the lateral region of the lower jaw area in the adult, crossing the aortic arches ventrally. Draining chiefly the muscles and skin of the intermandibular region, and receiving the facial vein or a branch thereof in *Salamandra* and various species of Salientia other than the Pipidae (see also p. 85). In *Pipa* possibly represented by the ramus communicans connecting the v. lingualis with the v. cava anterior.

Of the three it may be noted that the dorsal element supplied the original drainage for the tongue in *Salamandra*. In *Xenopus* and *Pipa* it is well developed although no tongue is present,* in *Rana esculenta* it is less conspicuous and no longer drains the tongue. No mention is made of such a vessel in *Bufo* and various species of *Rana* by Bhaduri (1931 and 1938), or in *Hyla* by Marriner (1906) or Gillies (1914).

The ventrolateral element is well developed in Ranidae, with a particularly strong facial component in some species (see p. 85); it is conspicuous in *Xenopus* larvae but poorly developed in the adult, and only a small and doubtful portion remains in *Pipa*.

It appears thus that the Pipidae stand apart from the Ranidae, Hylidae and Bufonidae in the better development of the dorsal element and the poorer development of the ventrolateral element of the external jugular. The ventral element is the most constant of the three.

It is considered by most authorities (*e.g.* Francis, 1934, van Gelderen, 1933) that the external jugular vein is the homologue of the inferior jugular

* The term v. lingualis in *Pipa* is a misnomer.

sinus of fishes and that the facial component is, at least in part, the homologue of the orbital, postorbital and hyoidean sinuses. This theory is borne out by the development of the vessels in *Xenopus*. The branchial branches of the external jugular are obviously homologous with the nutrient branchials which enter the inferior jugular sinus in Selachians.

Another point brought out by the development of *Xenopus* is the similarity during the early larval stages of the positions of the v. muscularis abdominis and the v. lateralis, and their common entry to the heart. When it first appears the v. muscularis abdominis is situated along the medial edge of the lateral plate mesoderm, just as (slightly later) the lateral vein is situated along the medial edge of the developing abdominal muscles. Both veins are ventral in position, only passing slightly more dorsally when approaching the heart, when the v. lateralis passes medial to the m. rectus cervicis and the v. muscularis abdominis lateral to it. However, in the very early stages the v. muscularis abdominis also has a connexion with the heart medial and ventral to the muscle (see text-fig. 7). Whether there is any significance in the similarity of the two vessels it is difficult to say without more detailed knowledge of the development in other Salientia.

Other Veins joining the Pronephric Sinus.

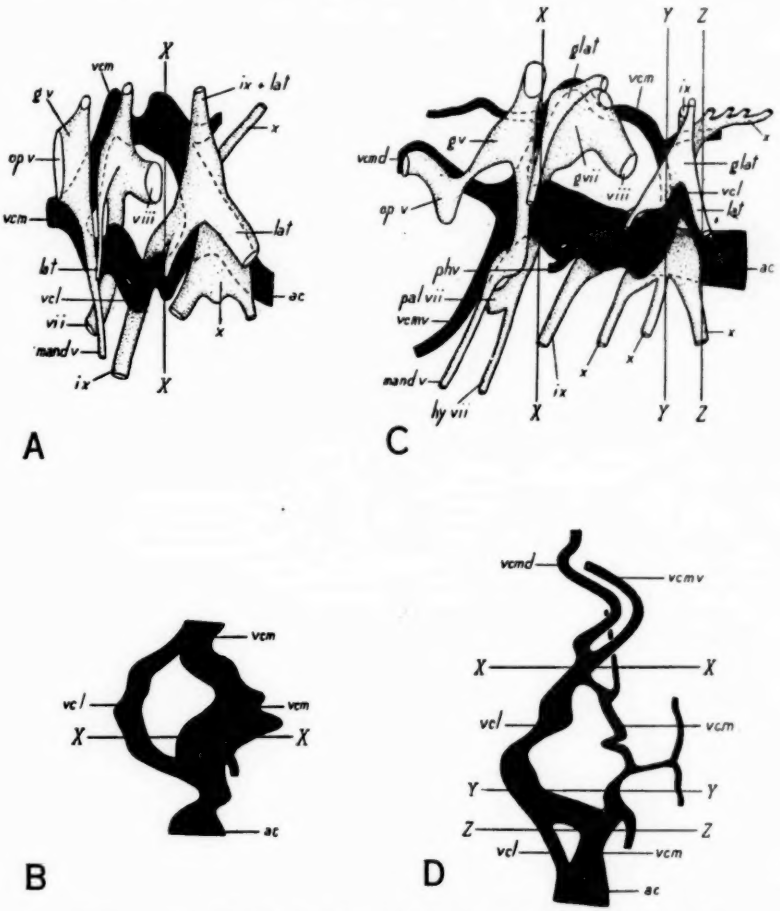
1. *The Branchial Veins.*

The lateral region of the branchial basket and filter apparatus is drained during the larval stages by a vein which runs along the lateral surface of the branchial basket and drains into the pronephric sinus. This vein receives small branches from the filter apparatus which emerge through foramina in the branchial basket; it crosses the aortic arches laterally and turns inwards round the posterior edge of the branchial basket to enter the pronephric sinus (Plates I to III; Plate VII, figs. 1 and 2). This is exclusively a larval vein and disappears at metamorphosis. It was mentioned by Weisz (1945 and 1945 *a*), who called it the lateral cutaneous vein, but since its drainage area is essentially the branchial basket and filter apparatus, and not the skin, the term "branchial vein" seems preferable.

2. *The Subclavian Veins.*

The fore limbs start developing at approximately 20 mm., and the first sign of the subclavian vein is a small blood-vessel flowing directly from the limb-bud into the pronephric sinus (Plate II). As the limb-bud develops the vessel elongates and becomes the brachial vein. At 44 mm. the vena cutanea magna is present draining the skin of the lateral region of the body,

and joining the brachial vein to enter the pronephric sinus as the subclavian vein (Plate III). After metamorphosis and the disappearance of the pronephric sinus the subclavian is directly continuous with the anterior vena cava, which is formed from the duct of Cuvier.



TEXT-FIGURE 9.—Reconstructions of the head-veins and cranial nerves in young tadpoles. A. Lateral view of left side, and B. ventral view of right side, of 5 mm. embryo (X–X marks position of section in Plate IV, fig. 1). C. Lateral view of left side, and D. ventral view of right side, of 6 mm. embryo (X–X marks position of section in Plate IV, fig. 2, Y–Y Plate IV, fig. 3, and Z–Z Plate IV, fig. 4). All × 109. For abbreviations see p. 99.

Development of the Anterior Cardinal Veins.

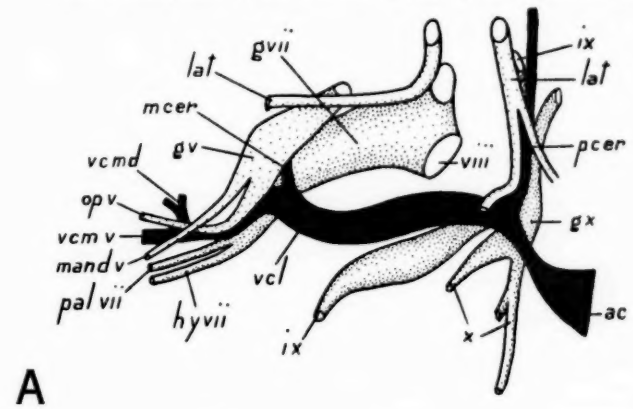
The anterior cardinal veins are formed very early in development and are first visible in 4 mm. embryos, *i.e.* just before the appearance of the posterior cardinals. At this stage each anterior cardinal vein receives a *vena capitis medialis* (situated internal and ventral to the roots of the cranial nerves) and passes posteriorly to empty into the developing pronephric sinus.

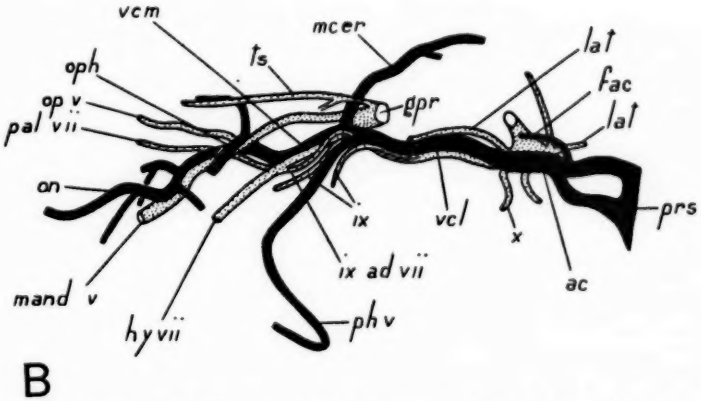
In 5 mm. embryos, in addition to the v. capitis medialis internal to the cranial nerve roots, there is also a *v. capitis lateralis* lateral to the auditory sac and nerves VII, VIII and IX (text-fig. 9, A and B; Plate IV, fig. 1). Of the two the v. capitis medialis is the broader, and is obviously the main element draining into the anterior cardinal. The v. capitis lateralis turns inward to join the v. capitis medialis at two points: (i) anteriorly between nerves V and VIII where they issue from their respective ganglia, and (ii) at a point between the vagus ganglion on the one hand, and the ganglia of the glossopharyngeal and posterior lateralis nerves on the other.*

In 6 mm. larvae both v. capitis medialis and lateralis are still present, but the v. capitis lateralis is better developed and extends further back (text-fig. 9, C and D). It has now three connexions with the v. capitis medialis: (i) the anterior one as in 5 mm. between nerves V and VII (Plate IV, fig. 2); (ii) a median one as in 5 mm. between the vagus ganglion on the one hand, and the posterior lateralis and glossopharyngeal nerves on the other (Plate IV, fig. 3); and (iii) a new posterior one behind the vagus ganglion (Plate IV, fig. 4). The v. capitis lateralis thus possesses a new portion lateral to the vagus ganglion. Of the two veins, the v. capitis lateralis is now the better developed, except for the short region lateral to the vagus ganglion. The v. capitis medialis receives several branches from the surface of the brain and extends forwards in front of the anterior connexion with the v. capitis lateralis. In this region it is made up of two elements. Of these one passes through the dorsal region of the orbit close to the ophthalmic profundus nerve and drains the lateral surface of the anterior region of the brain, thus constituting a *v. cerebralis anterior.* The other element passes through the ventral region of the orbit close to the ramus mandibularis V and drains the eye. In the anterior region of the auditory sac the v. capitis lateralis receives a short *pharyngeal vein* from the pharynx.

In 7 and 8 mm. larvae (text-fig. 10, A; Plate I) the portion of the

* At this stage the vagus ganglion is easily distinct from the rest of the vagus-glossopharyngeus-lateralis complex. The lateralis ganglion is distinct from the glossopharyngeus posteriorly, but more difficult to distinguish anteriorly.





TEXT-FIGURE 10.—Reconstructions of head-vein and cranial nerves in lateral view of A. 8 mm. tadpole (× 120), and B. early metamorphosis (× 15). For abbreviations see p. 99.

v. capitis medialis posterior to the trigeminal nerve is absent. At this stage then the anterior cardinal receives a head-vein of compound origin, the anterior portion of which arose from the v. capitis medialis and passes medial to the trigeminal nerve, and the posterior portion of which arose from the

v. capitis lateralis and is situated lateral to the auditory sac and the roots of cranial nerves VII to X. This head-vein receives, in addition to the pharyngeal vein mentioned above, three cerebral veins:

(i) *The anterior cerebral vein*, which is the anterior continuation of the dorsal element of the v. capitis medialis as described in 6 mm.

(ii) *A median cerebral vein* joining the v. capitis lateralis in the region of the ganglion prooticum. This vein is formed from part of the v. capitis medialis and from its anterior connexion with the v. capitis lateralis. It passes between the ganglia of V and VII.

(iii) *A posterior cerebral vein* which passes through the centre of the combined vagus-glossopharyngeus-lateralis ganglion to join the v. capitis lateralis (Plate VI, fig. 4). This vein is the remains of the original median connexion between the v. capitis medialis and lateralis.

In 10 mm. and older larvae the posterior cerebral vein has disappeared entirely. The original anterior cerebral vein is very much shorter and no longer reaches the brain, draining instead various regions in the orbit. Hereafter it is known as the *ophthalmic vein*. A median cerebral vein is present but has changed its position. The ganglia of V and VII are now fused as the prootic ganglion, and the median cerebral vein, instead of passing between V and VII, passes over the dorsal surface of the entire ganglion (but ventral to the truncus supraorbitalis) (text-fig. 10, B; Plate VII, fig. 1). This becomes the cerebral vein of the adult.

The course of the anterior cardinal and head-vein of a typical older embryo will now be described, for the sake of convenience starting from the posterior end and working forwards (text-fig. 10, B; Plates II and III).

The *anterior cardinal vein* can be traced forwards from the pronephric sinus between the myotomes and the dorsolateral edge of the branchial basket on to the lateral surface of the vagus ganglion. During this part of its course it receives several small branches:

(i) One or two small branches from the myotomes and from the muscles of the scapula, which probably form the v. occipitalis and the v. vertebralis of the adult.

(ii) A narrow vein from the skin accompanying the posterior lateralis nerve and joining the anterior cardinal posterior to the musculus depressor mandibulae. This vein is not apparent until the early stages of metamorphosis. From its position and point of junction with the anterior cardinal it is evident that it becomes the *v. facialis* of the adult. After metamorphosis it is better developed and takes over the drainage of the thymus gland.

The part of the head-vein developed from the *v. capitis lateralis* (*i.e.* the part behind the prootic ganglion) can be traced round the lateral surface of the inner ear in close juxtaposition to the glossopharyngeal nerve, which it eventually crosses dorsally, then in front of the auditory region it bends inward and comes to lie lateral to the ganglion prooticum. During this part of its course two branches are received:

(iii) The *pharyngeal vein*, joining the v. capitis lateralis just anterior to the fenestra ovalis. Drains the lateral and dorsal regions of the pharynx, and also the thymus gland (Plate VII, fig. 1). This is a larval vein and disappears at metamorphosis, when the drainage of the thymus is taken over by the facial vein.

(iv) The *cerebral vein*, joining the v. capitis lateralis in the region of the foramen prooticum (Plate VII, fig. 1). Consists of (*a*) an anterior branch draining the dorsal region of the brain, (*b*) a median branch from the pituitary body and (*c*) a posterior branch draining the dorsolateral surface of the brain. After the junction of these the cerebral vein crosses the ganglion prooticum dorsally and the truncus supraorbitalis ventrally, and leaves the skull through the foramen prooticum to join the v. capitis lateralis.

After this that part of the head-vein developed from the *v. capitis medialis* (*i.e.* the part in front of the prootic ganglion) can be traced forwards with the hyomandibular, ophthalmic profundus and palatine nerves over the ventral surface of the ventrolateral process of the palatoquadrate to the region of the subocular fenestra. Here it receives the v. ophthalmica.

(v) *Ophthalmic vein*. Corresponds to the dorsal element of 6 mm. larvae and to the v. ophthalmica of the adult. Drains the eye and muscles in the dorsal region of the orbit, and crosses dorsally over the optic and mandibular nerves. Receives a branch from the dorsal surface of the cranium.

Anterior to this point the v. capitis medialis corresponds to the ventral element of 6 mm. larvae and to the v. orbito-nasalis of the adult. It crosses the optic nerve ventrally and the mandibular nerve medially, and can be traced through the subocular fenestra over the dorsal surface of the processus muscularis of the palatoquadrate to the anterior region of the snout. It drains the nasal organ, tentacle, skin, dorsal buccal cavity, and the muscles of the lower jaw and ceratohyoid, and receives a branch from the ventral region of the eye and its muscles.

After metamorphosis the facial vein becomes better developed and

takes over the drainage of the thymus gland; the pharyngeal vein disappears, and a portion of the head-vein posterior to the region of the prootic ganglion becomes incorporated in the auditory capsule where it accompanies the hyomandibular nerve and passes dorsally over the columella and middle ear. The entire vein is then known as the *internal jugular* and, as has been shown above, is a vessel of compound origin: the portion anterior to the ganglion prooticum being formed from the v. capitis medialis, the portion between the ganglion prooticum and the vagus ganglion from the v. capitis lateralis, and the portion posterior to the vagus ganglion from the anterior cardinal. The internal jugular opens into the v. cava anterior, which is formed from the shortened duct of Cuvier after the disappearance of the pronephric sinus.

Discussion.

The course of the head-vein ("Stammvene") in well-grown tadpoles has been described by Paterson (1939 and 1942), and her description does not differ in any essential details from the present one. She also considered the anterior portion of the vein to represent a v. capitis medialis, but does not deal with stages young enough to show the latter in its entirety, and so was not able to establish the posterior limit of the v. capitis medialis accurately. In her diagram (fig. 9, 1942) she wrongly shows the v. capitis medialis as extending backwards as far as the junction with the pharyngeal vein. Paterson (p. 284) assumes that the pharyngeal vein (*i.e.* the vein "from the dorsal wall of the pharynx") gives rise to the cutaneous vein of the adult, but it has been shown above that both brachial and cutaneous veins open at first into the pronephric sinus, and, during the stages immediately preceding metamorphosis, exist together with the pharyngeal vein (Plate III). The pharyngeal vein disappears at metamorphosis and does not persist in the adult stage.

The vv. capitis medialis and lateralis were clearly defined by Goodrich (1930, pp. 532–535), who states that the v. capitis medialis in Craniates lies medial to the cranial nerves and auditory sac and drains the brain. It is soon "more or less completely replaced by another more lateral longitudinal vein, the v. capitis lateralis, which develops outside the cranial wall and flows into the anterior cardinal behind the vagus nerve". He states, however, that "occasionally (as in Cyclostomata, most Selachia, Polypterini, and Anura) the v. capitis lateralis continues forward to the orbit outside the trigeminal nerve". It is evident from the description above that conditions in *Xenopus* approach more nearly to those in Urodeles and the majority of Craniates in that the anterior portion of the head-vein is derived from a v. capitis medialis and is *inside* the trigeminal nerve.

Goodrich also defines the three cerebral veins: (i) an anterior cerebral from the eye and fore-brain, (ii) a median cerebral from the middle region of the brain and the cerebellum, joining the head-vein between the roots of V and VII, and (iii) a posterior cerebral from the remainder of the hind-brain joining the head-vein near the vagus nerve. Van Gelderen (1933) states that "Die Dipnoer, Amphibien und Amnioten bekommen alle eine richtige V. cerebralis media vera, die sich dem N. trigeminus aboral auschliesst, jedoch oft nachher verödet". It has been shown that the three cerebral veins are present in the young stages of *Xenopus*, but that the anterior and posterior disappear later. Moreover the cerebral vein of the adult is not a true "V. cerebralis media vera", since it changes its position during development and comes to emerge anterodorsal to the trigeminal nerve. This latter condition resembles that of Saurians and Ophidia (van Gelderen, 1933).

The course of the facial vein in *Xenopus* is worthy of note. According to Bhaduri (1931 and 1938) the facial veins of Salientia can be divided into three categories:

(*a*) Those in which the facial vein flows direct into the cutaneous, *e.g.* *Rana esculenta* and *R. temporaria.*

(*b*) Those in which the facial vein has two outlets, one to the cutaneous vein and the other to the external jugular, *e.g. R. tigrina* and various other Indian species of *Rana.*

(*c*) Those in which the facial vein flows into the external jugular only, *e.g. Hyla aurea, Bufo melanostictus* and *Cacopus systoma.*

It appears that *Xenopus* provides a fourth category, where the facial vein flows into the internal jugular. It is probable that *Pipa americana* belongs to the same group, since in a rather brief account Grönberg and Klinckowström (1893) describe a "V. cutanea anterior" as joining the v. jugularis interna.

Discussion of the Classification of the Salientia and the Position of the Pipidae Therein.

1. *Classification.*

The most recent comprehensive classification of the Salientia is that of Noble (1931), who divided the group into five suborders based chiefly on the nature of the vertebrae, supported by the presence or absence of ribs and the structure of the pectoral girdle. This classification was a revision of previous ones and an attempt at a more natural basis. Although Noble's

five suborders still stand, a number of changes have been made in the families as a result of more recent investigations.

The classification as accepted at the present time is as follows:

Order: *Salientia.*
- *Suborder* 1: *Amphicoela.*
  - Family 1: Liopelmidae.
- *Suborder* 2: *Opisthocoela.*
  - Family 2: Discoglossidae.
  - Family 3: Pipidae.
- *Suborder* 3: *Anomocoela.*
  - Family 4: Pelobatidae.
- *Suborder* 4: *Procoela.*
  - Family 5: Bufonidae.
  - Family 6: Leptodactylidae.
  - Family 7: Brachycephalidae (Atelopodidae).
- *Suborder* 5: *Diplasiocoela.*
  - Family 8: Ranidae.
  - Family 9: Heleophrynidae.
  - Family 10: Rhacophoridae.
  - Family 11: Microhylidae.

In Noble's classification the Leptodactylidae were included in the family Bufonidae, but according to Parker (1940) the group should be given family status.

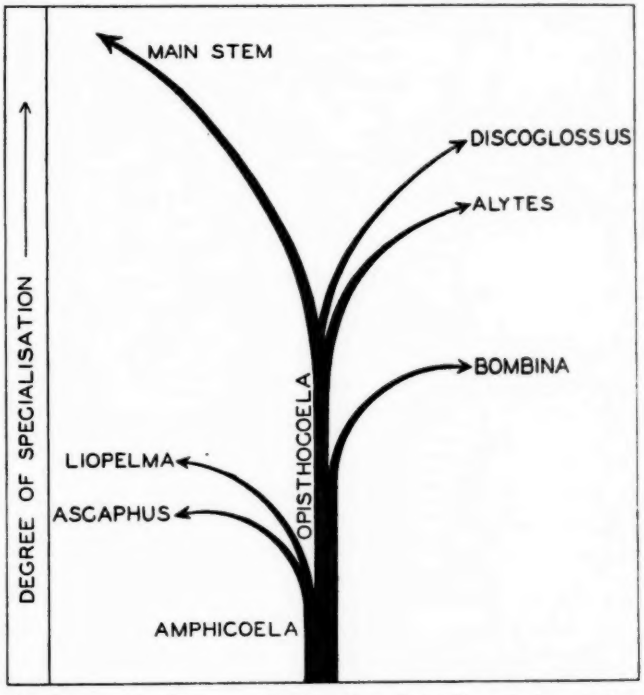
The position of *Heleophryne* has long been a matter of dissension. Noble placed the genus in a sub-family of the Bufonidae, but according to recent workers (du Toit, 1930; Hoffman, 1930; and Latsky, 1930) it cannot definitely be referred to any family of the Salientia. From a recent discussion with Professor C. A. du Toit, *Heleophryne* should be placed in a separate family, the Heleophrynidae, which according to Latsky (1930) belongs among the Diplasiocoela.

According to the rules of biological nomenclature the Rhacophoridae take preference over Noble's Polypedatidae (Parker, 1934, Hoffmann, 1942), and the Microhylidae over Noble's Brevicipitidae (Parker, 1934).

Of the five suborders Noble considered the Amphicoela, Opisthocoela and Anomocoela to be more primitive than the Procoela and Diplasiocoela. This conclusion was based on the evidence of the thigh musculature and tendons as well as that of the vertebral column, pectoral girdle and ribs. Each group, however, possesses members which have become specialised in particular directions.

The most primitive members of the Salientia are to be found among the Liopelmidae, including the genera *Ascaphus* and *Liopelma*, and the

Discoglossidae, including *Alytes*, *Bombina* (= *Bombinator*), *Discoglossus* and *Barbourula*. The thigh musculature of *Ascaphus* and *Bombina* is "sufficiently generalised to form a prototype for all higher forms" (Noble, 1922). Various features of the Liopelmidae (the amphicoelous vertebrae, the presence of two coccygeal muscles, the single coracoscapula, and the presence of three pairs of cartilages in the inscriptio tendinea of the rectus



TEXT-FIGURE 11.—Diagram indicating the relationships of the primitive members of the Salientia. From Slabbert and Maree (1945).

abdominis muscle) show similarities to the Urodeles and indicate that they are the most primitive living members of the Salientia (Noble, 1922 and 1925). This conclusion is supported by Slabbert and Maree (1945) on the evidence of the cranial anatomy, who also maintain that *Bombina* is the most primitive member of the Discoglossidae. A diagram showing the relations of the primitive members of the Salientia as given by the latter authors is reproduced here (text-fig. 11). The primitive nature of the Liopelmidae and Discoglossidae is supported by the persistence of the postcardinal veins in

Ascaphus (Noble, 1925) and in *Bombina*, *Discoglossus pictus* and *Alytes obstetricans* (one specimen out of five) (Howes, 1888, O'Donoghue, 1931).

The Pipidae were considered by Noble (1922) and de Villiers (1929) to have arisen from a common stem with the Discoglossidae. If included in the diagram given (text-fig. 11) they would arise from the main stem above *Discoglossus*, and the Pelobatidae soon after.

Of the remaining groups the evidence of the tendons of the thigh (Noble, 1922) shows the Procoela to be more primitive than the Diplasiocoela.

The presence or absence of teeth, the dilation of the diapophyses of the sacral vertebrae, and the degree of ossification of the skull were considered by Noble (1922) to be unreliable bases for classification, since parallel modifications occur in each suborder.

2. *Position and Characters of the Pipidae.*

The Pipidae, including the six genera *Xenopus*, *Hymenochirus*, *Pseudohymenochirus*, *Pipa*, *Protopipa*, and the newly described *Hemipipa* (Parker, 1940 *a*), as shown above, are considered by most authors to belong to one of the more primitive groups of the Salientia. The primitive features of the Pipidae may be briefly summarised as follows:—

(i) The opisthocoelous vertebrae. In other suborders they tend to become either procoelous or diplasiocoelous (Noble, 1922).

(ii) Ribs distinct in larvae, but fused with the vertebrae in the adult. In the Discoglossidae the ribs remain free throughout life. In all other Salientia ribs are absent (Noble, 1922, Ridewood, 1897 *a*).

(iii) Structure of the pectoral girdle. Of arcifero-firmisternal type in *Xenopus* and *Pipa* (although firmisternal in *Hymenochirus*) (Noble, 1922, de Villiers, 1929). The primitive condition is considered to be arciferal as seen in most Opisthocoela, in the Anomocoela, and most Procoela; but tending to become arcifero-firmisternal in the Pipidae among Opisthocoela, arcifero-firmisternal to firmisternal in the Procoela, and firmisternal in the Diplasiocoela.

Other primitive features of the pectoral girdle of the Pipidae are considered by de Villiers (1929) to be the absence of an episternum (also absent in the Liopelmidae, just present in the Discoglossidae), the large size of the procoracoid relative to the clavicle, and the large size of the cleithrum.

The structure of the girdle seems to indicate that *Xenopus* is more primitive than *Pipa*, and *Pipa* more primitive than *Hymenochirus*, although all three should probably be derived independently

from Pro-Aglossa. *Pseudohymenochirus* appears to be closely allied to *Hymenochirus*, and *Protopipa* and *Hemipipa* to *Pipa*.

(iv) The development of the skull. Kotthaus (1933) maintains that the following features in *Xenopus* are primitive: the undivided foramen acusticum plus endolymphaticum plus perilymphaticum, the limited development of the skull roof, and the nature of Meckel's cartilage.

(v) The musculature of the pectoral region in the Pipidae and Anomocoela is primitive compared with that of the Procoela and Diplasiocoela, yet not so primitive as that of the Discoglossidae (quoted by Noble from the work of Anthony and Vallois, 1914).

(vi) Various characters of the thigh muscles (Noble, 1922), namely:
- (*a*) Adductor longus not differentiated from pectineus.
- (*b*) Accessory head of iliacus externus retained.
- (*c*) Adductor magnus consisting of two separate muscles, and without an accessory head.
- (*d*) Obturator externus well developed.
- (*e*) Sartorio-semitendinosus broad and superficial.
- (*f*) Sartorius not or only partially distinct.

(vii) Various characters of the body muscles (Grobbelaar, 1924 *a*):
- (*a*) The nature of m. rectus abdominis, stretching from the pelvic region to the hyoid apparatus.
- (*b*) Ileolumbar not divided into median and lateral portions.
- (*c*) Absence of rhomboideus posterior.
- (*d*) General undifferentiated nature of muscles.

(viii) The muscles connected with the branchial and hyoid skeleton of the larva are simpler in the Pipidae than in the "Phaneroglossa" (Paterson, 1939, Edgeworth, 1935).

(ix) The arrangement of the cranial nerves resembles that of Urodeles more than that of "typical Anura" (Paterson, 1939).

(x) The paired opercular opening of the tadpole (Ridewood, 1897).

(xi) The pelvic embrace of the male during breeding. Found in the Liopelmidae, Discoglossidae, Pipidae and Pelobatidae. All others have a pectoral embrace (Noble, 1931) with a few exceptions.

It has become increasingly evident, however, that the Pipidae are not only primitive in many features, but are also *neotenic*. This is obvious at once from their aquatic habitat, and on closer study further evidences of a neotenic nature become apparent. It appears that the Pipidae among the Salientia to a certain extent present a parallel to the Perennibranchiata among the Urodeles.

The neotenic features of the Pipidae may be summarised as follows:

(i) The maintenance of an aquatic habitat throughout life.

(ii) The maintenance of lateral line sense-organs in the adult. Also found in the aquatic *Bombina* (Escher, 1925, Noble, 1931) and *Ceratophrys laevis* (Noble, 1931), and in *Leptobrachium monticola*, *Rana hexadactyla*, and various species of *Pseudis* (Boulenger, 1893, quoted by Ridewood, 1897).

(iii) The poorly developed fore limbs, which are not used for locomotion, but merely for feeding.

(iv) The nature of the external gills, where the development is not completed. (Absent in *Bombina*, Kerr, 1919, and reduced in *Hyla arborea*.)

(v) The absence of internal gills. Also absent in Urodeles.

The Pipidae are, however, not only primitive and neotenic, but possess many characteristics of a specialised nature. It is this mixture of the primitive and the specialised which has for so long puzzled systematists. It is considered by the writer that the Pipidae are primarily primitive and neotenic, and that those specialisations which are common to the whole family are adaptations connected with the aquatic habitat and so are a result of neoteny. These specialisations are listed below:

(i) The absence of a tongue. Considered by Noble (1922) to be an aquatic modification. He refers to *Batrachophrynus* (Bufonidae), which also is aquatic and has only a slight indication of a tongue. According to Ridewood (1897) and Edgeworth (1935) the evidence of the laryngeal muscles shows the Pipidae to be descended from tongued forms.

(ii) Other features which according to Ridewood (1897) are possibly connected with the absence of a tongue, and thus also a result of the aquatic habitat, are the complexity and sexual dimorphism of the larynx, the elongated bronchi, the union of the Eustachian tubes and the specialisation of the hyoid apparatus.

(iii) The structure of the auditory apparatus. The Pipidae are characterised by the large size of the plectral apparatus and the small size or complete absence of the operculum, a condition undoubtedly associated with the aquatic habitat. The general structure of the auditory apparatus and surrounding regions of the skull is more specialised in *Hymenochirus* than in *Pipa* or *Xenopus* (de Villiers, 1932).

(iv) The absence of eyelids is undoubtedly an aquatic modification. Lower eyelids are, however, retained by *Pseudohymenochirus* (Noble, 1931).

(v) The thigh muscles have, according to Noble (1922), reached their maximum development for swimming, although special swimming muscles have not appeared.

(vi) The disappearance of the pyriformis muscle is according to Green (1931) the result of the aquatic habitat. It is reduced in *Xenopus*, absent in *Pipa* and *Hymenochirus*, thus supporting the theory that *Xenopus* is the most primitive of the three.

(vii) The so-called "diaphragm" of *Xenopus* and *Pipa*, which is derived from three sources instead of one as in *Rana*, is associated with the aquatic habitat and enables the lungs to be filled and emptied more rapidly (Beddard, 1895, Green, 1931).

(viii) The fusion of the urostyle with the sacrum in *Hymenochirus* and *Xenopus* is, according to Green (1931), an aquatic feature.

(ix) The epipubis of *Xenopus*, according to Green (1931), has a hydrostatic function similar to the ypsiloid cartilage of aquatic newts.

(x) A number of specialised features of the skull have been listed by Noble (1931) and Kotthaus (1933), which are difficult to attribute to any particular cause, and so will not be described in detail here.

The remarkable difference in the life-histories of *Xenopus* and *Pipa* has often been noted. The tadpole of *Xenopus* is an agile fish-like creature, particularly well adapted to its active type of life (*e.g.* filter apparatus, tentacles, etc.). The larva of *Pipa* (and of the closely related *Protopipa* and *Hemipipa*) passes through its developmental stages in dermal pockets on the back of the mother.

Noble (1925 *a*) has pointed out that closely related genera of Salientia generally have the same type of life-history, and quoted as an example the case of *Pipa* and *Protopipa*. In 1931 on these grounds he divided the Pipidae into two sub-families:

(*a*) The *Pipinae*, including the South American *Pipa*, *Protopipa* and *Hemipipa*.

(*b*) The *Xenopinae*, including the African *Xenopus*, *Hymenochirus* and *Pseudohymenochirus*, of which it is assumed that the two latter genera have a similar life-history to *Xenopus*.

It would be interesting to compare the detailed anatomy of the larvae of these two sub-families. One would expect structural similarities within a family, although the life-history is so different. Unfortunately the writer has as yet been unable to obtain specimens of larval stages of the Pipinae.

3. *Evidence from the Vascular System of* Xenopus.

The general plan of the vascular system of *Xenopus* on the whole conforms well to the typical Salientian type. This has been shown not only in the development of the venous system, but also in the development of the arteries (Millard, 1945) and in the adult vascular system (Millard, 1941). Where differences do occur the vascular systems can be compared more profitably with Urodeles, as for instance in the arrangement of the external jugular veins, the veins of the hind limbs, and the development of the arterial system of the external gills. The Urodeles as a group are primitive *and* neotenic; and it is not always an easy matter to distinguish between primitive and neotenic features. To settle the question, comparison would be necessary with a truly primitive Salientian type such as *Ascaphus* or *Liopelma*, which is impossible at the moment due to the absence of literature on vascular development in these forms.

Features in which *Xenopus* may be considered primitive and/or neotenic may be listed as follows:

(i) Persistence of right omphalomesenteric vein and subintestinal vein in the adult.

(ii) The arrangement of the hind limb veins. During development the ischiadic veins do not connect directly with the lateral post-cardinals as in *Rana*, but with the anastomoses between the latter and the abdominal vein. In the adult the main blood-flow from the lower limb (vena poplitea) is postaxial as in Urodeles, and not preaxial as in *Rana*.

(iii) The arrangement of the external jugular veins in both the larval and adult stages shows a closer resemblance to Urodeles than to *Rana*.

(iv) The origin of the "head-vein" or vena jugularis interna. The anterior portion is derived from a vena capitis medialis as in Urodeles, and not from a vena capitis lateralis as in most Salientia.

(v) The vena bulbi cordis posterior of the adult enters the sinus venosus. In *Rana* this condition pertains in the larva, but in the adult the v. bulbi cordis posterior becomes secondarily connected with the abdominal vein.

(vi) The presence in early developmental stages of a continuous first (mandibular) aortic arch, and the rudiment of a second (hyoidean).

(vii) The development of the aortic arches and arterial supply to the external gills. Aortic arches 3 and 4 are laid down each with a primary and secondary vessel, of which the latter supplies the external gill but has its development arrested at an early stage. The primary vessel becomes the adult aortic arch without "splitting" into afferent and efferent portions as in *Rana*.

(viii) The persistence of the larval artery supplying the musculares constrictores branchiales as an accessory branch of the carotid arch in approximately 42 per cent. of the adults.

It may thus be concluded that the development and anatomy of the vascular system supports the contention put forth above that *Xenopus* is primarily primitive and neotenic. In the specialised features of the adult vascular system, namely the arrangement of the hind limb veins and external jugular veins, *Pipa* agrees with *Xenopus*, and so far as is known at present the conclusion may be applied to the Pipidae as a whole.

As in the general anatomy, so in the vascular system, specialisations are found comparable neither with the Urodeles nor with the higher Salientia. Further study may show that some of these are common to the Pipidae as a whole and consequently are a result of neoteny, others may be peculiar to *Xenopus* and possibly related to the unusual feeding methods of the larva. Such specialised features are listed below:

(i) Independent origin of hepatic vein.

(ii) Unpaired origin of posterior part of abdominal vein.

(iii) Early disappearance of ductus Botalli.

(iv) Preponderance of third aortic arch over fourth and fifth during larval stage.

(v) Blood supply of filter apparatus of the larva, which is highly specialised, although on a similar ground-plan to that of *Rana*. The arteries arise from the aortic arches. The veins drain into the external jugular, except for the branchial vein (unrepresented in *Rana*), which enters the pronephric sinus.

(vi) The reduction in importance and calibre of the arteria cutanea magna as compared with that of most Salientia. If it is agreed that *Xenopus* is more primitive than *Pipa*, this is a secondary feature reaching its culmination in *Pipa* where the arteria cutanea magna is absent altogether.

Summary.

1. In early developmental stages two omphalomesenteric veins open into the heart. Later these break up into capillaries in the liver. The afferent portion of the left vein becomes the subintestinal and persists in the adult. The afferent portion of the right vein persists in the adult as part of the hepatic portal system.

2. The hepatic vein arises independently and not as a branch of either omphalomesenteric.

3. Two median postcardinal veins are laid down median to the Wolffian

ducts. These veins fuse in the mid-line posteriorly to form the median channel of the mesonephric sinus (interrenal vein) and open into the pronephric sinuses anteriorly. Two lateral postcardinals appear lateral to the Wolffian ducts and become connected with the median postcardinals by anastomoses to form the lateral channels of the mesonephric sinus. They connect with the caudal vein posteriorly and form the renal portal system of the adult.

4. The posterior vena cava grows back from the hepatic vein to join the right median postcardinal, which is continuous with the interrenal vein. The posterior vena cava completely takes over the drainage from the mesonephroi when the anterior portions of median and lateral postcardinals disappear at metamorphosis.

5. The abdominal vein of the adult develops from (*a*) a median vessel on the posterior ventral abdominal wall which connects with the caudal vein by anastomoses, and (*b*) two lateral veins on the anterior abdominal wall which fuse posteriorly and open anteriorly into the sinus venosus. At metamorphosis the anterior portions of the lateral veins disappear and the abdominal vein acquires a secondary connexion with the hepatic portal system.

6. Ischiadic and femoral veins acquire connexions with one of the anastomoses between abdominal and caudal veins.

7. The veins of the ventral region of the head can be resolved into three main elements, viz. a dorsal (v. jugularis externa), a ventral (v. muscularis-thyroidea) and a ventrolateral (v. muscularis abdominis), comparable with similar elements in Urodeles. The ventral element appears only at metamorphosis. The ventrolateral element is preponderantly a larval vein which becomes reduced in importance at metamorphosis. The dorsal element is present in both larva and adult.

8. The branchial basket is drained (*a*) by a number of branches which flow into the v. jugularis externa, and (*b*) by a branchial vein which opens into the pronephric sinus. All these vessels disappear at metamorphosis.

9. The subclavian vein, consisting of brachial and cutaneous components, opens into the pronephric sinus, and is continuous with the anterior vena cava after metamorphosis.

10. The dorsal region of the head is drained in young stages by a vena capitis medialis, of which the posterior part is later replaced by a v. capitis lateralis which joins the anterior cardinal sinus. This composite vein becomes the internal jugular of the adult. Three cerebral veins are present in the young stage, of which only the median one persists as a branch of the internal jugular but changes its position. The facial vein opens into the anterior cardinal.

11. Existing literature on the classification of the Salientia and the position of the Pipidae therein is discussed, and it is concluded that the Pipidae are primarily primitive and neotenic, and that those specialisations which do occur are a result of neoteny. This is supported by the evidence of the vascular system.

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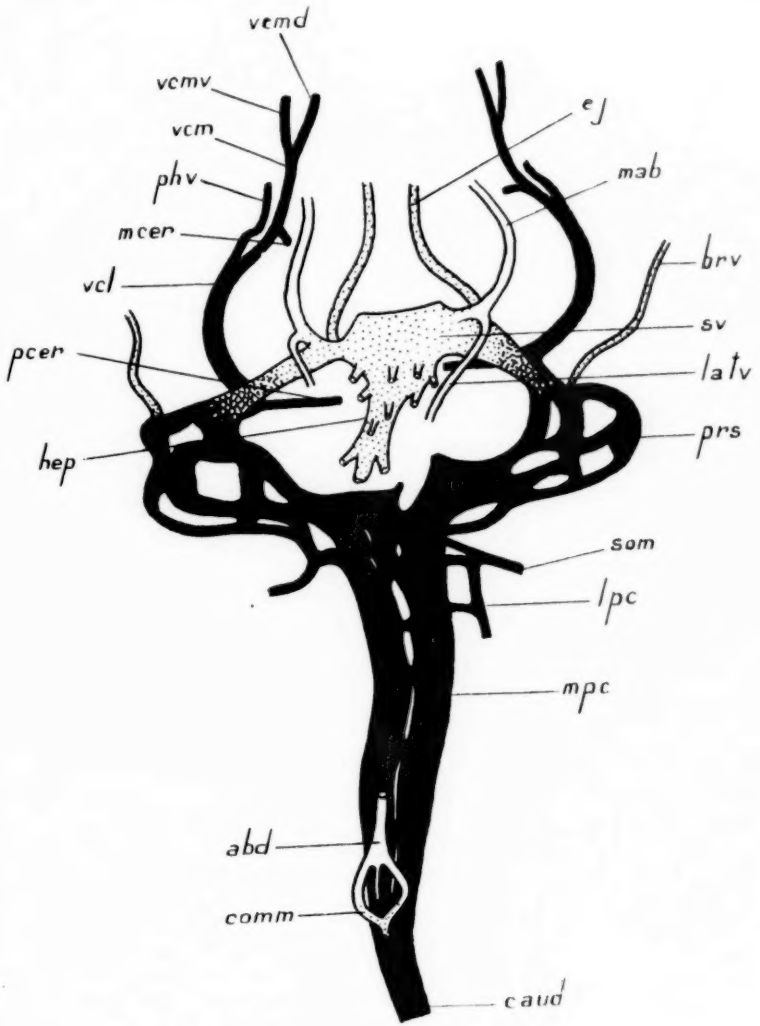

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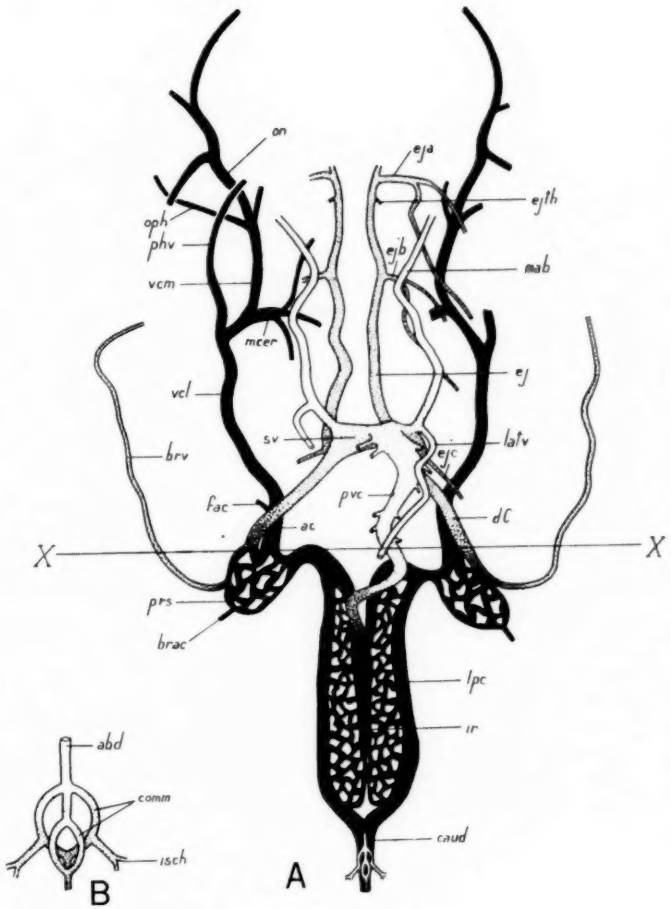
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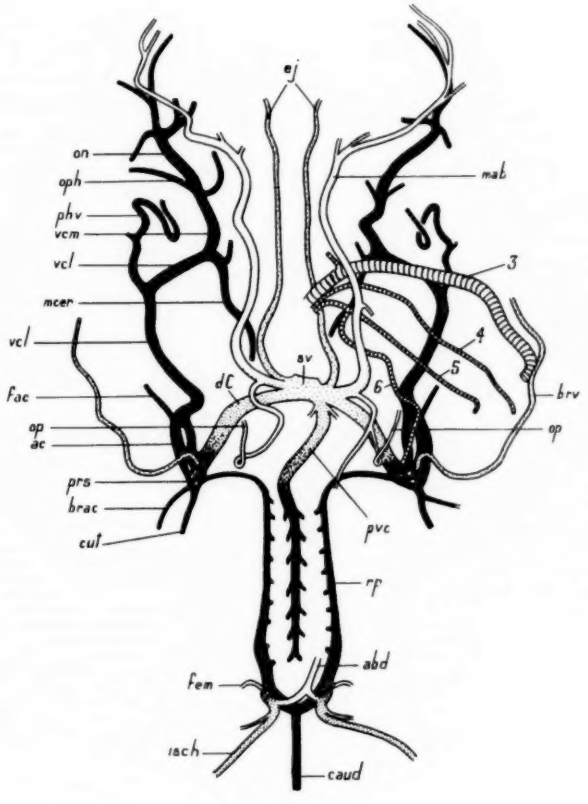
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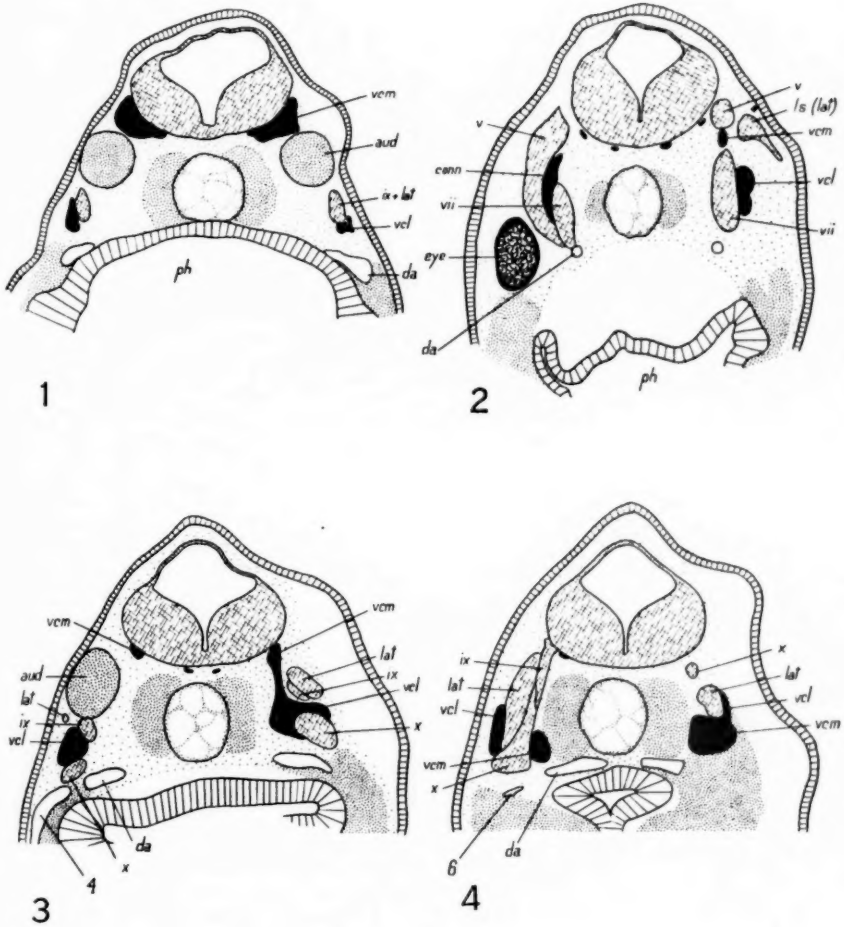
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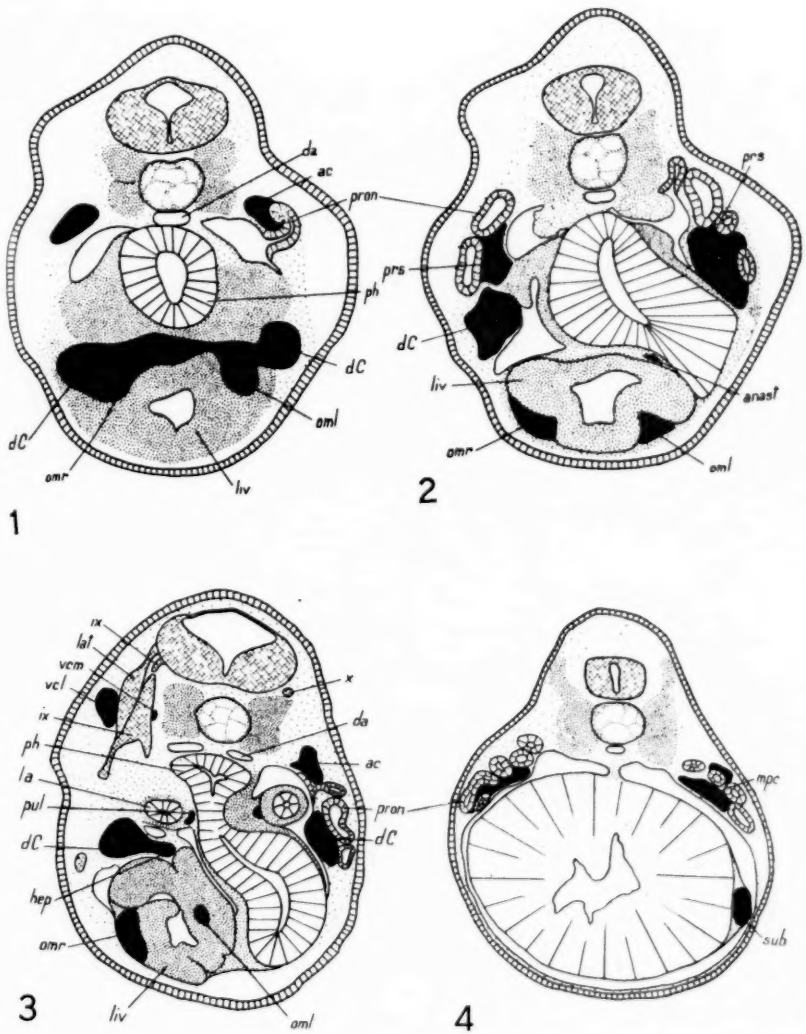

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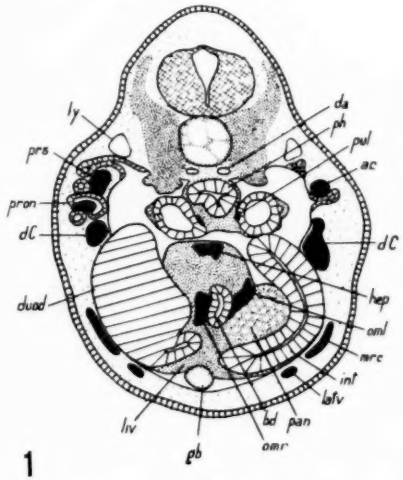

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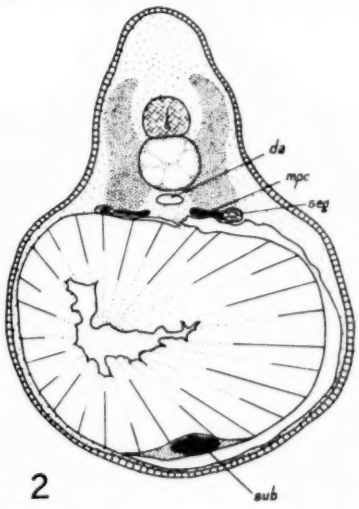

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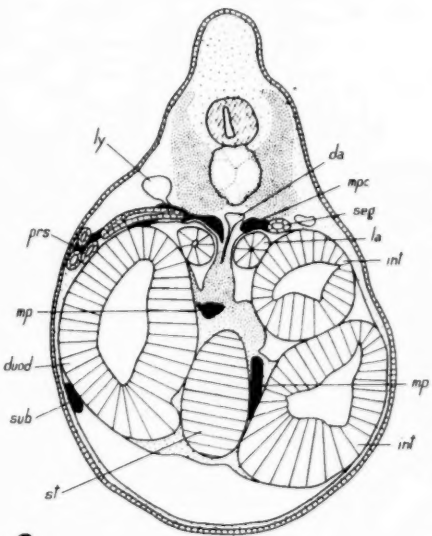

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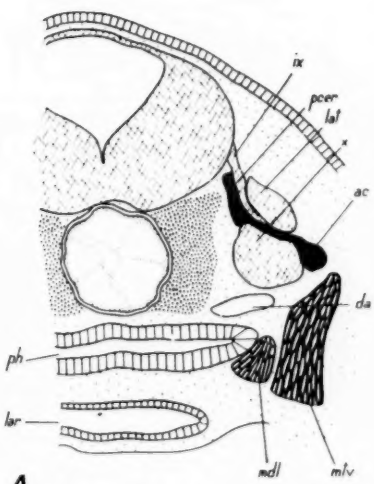

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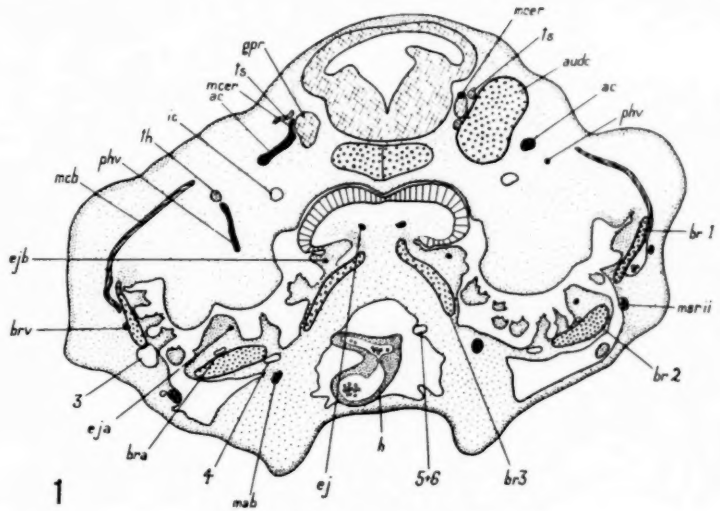
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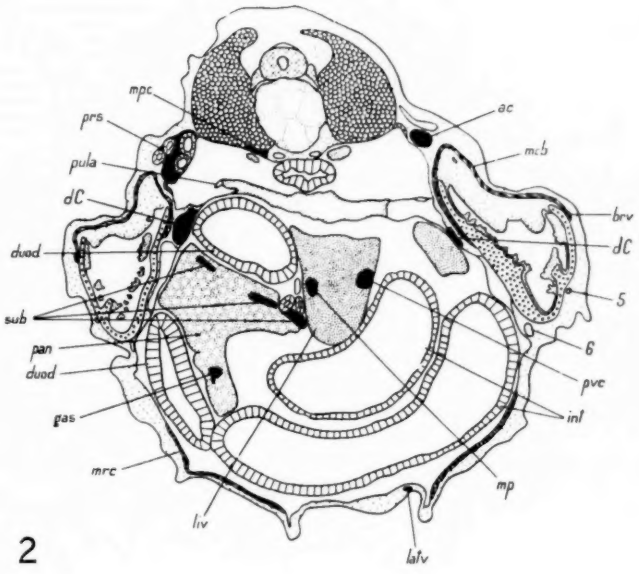
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DESCRIPTION OF PLATES.

NOTE.—The reconstructions in Plates I–III are shown in ventral view. The sections in Plates IV–VII are drawn in anterior view, so that the right side of the animal is on the left of the diagram and *vice versa*.

PLATE I.

Reconstruction of venous system of 8 mm. tadpole. Hepatic portal system not shown. Venous network of pronephros diagrammatic. × 90.

PLATE II.

A. Reconstruction of venous system of 24 mm. tadpole. Hepatic portal system not shown. The branches of the right anterior cardinal and the left external jugular veins are shown in detail. Venous network of pro- and mesonephros diagrammatic. X-X indicates position of section in Plate VII, fig. 2. × 19.

B. Posterior region of abdominal vein more highly magnified than in A.

PLATE III.

Reconstruction of the venous system of tadpole commencing metamorphosis. Hepatic portal system and branches of external jugular vein not shown. The left aortic arches are included to indicate their position relative to the veins. × 11.

PLATE IV.

Fig. 1.—Section through 5 mm. embryo, showing position and comparative sizes of vena capitis medialis and vena capitis lateralis. Compare with Plate IV, fig. 3. Section taken at level X–X in text-figure 9, A and B. × 75.

Fig. 2.—Section through 6 mm. tadpole, passing through anterior connexion between right vena capitis medialis and vena capitis lateralis, and just posterior to left connexion. Pharynx displaced during sectioning. Section taken at level X–X in text-figure 9, C and D. × 75.

Fig. 3.—Section through 6 mm. tadpole, passing through median connexion between left vena capitis medialis and vena capitis lateralis, and slightly anterior to right connexion. Section taken at level Y–Y in text-figure 9, C and D. × 75.

Fig. 4.—Section through 6 mm. tapdole, passing through posterior connexion between left vena capitis medialis and vena capitis lateralis, and slightly anterior to right connexion. Section taken at level Z–Z in text-figure 9, C and D. × 75.

PLATE V.

Fig. 1.—Section through 6 mm. tadpole, showing entry of omphalomesenteric veins into heart, and commencement of left pronephros. × 67.

Fig. 2.—Section through 6 mm. tadpole, showing position of right and left omphalomesenteric veins and pronephric sinuses. × 67.

Fig. 3.—Section through 6·5 mm. tadpole, showing entry of hepatic vein into right duct of Cuvier, and position of right and left omphalomesenteric veins. Section taken at level X–X in text-figure 1, A. × 54.

Fig. 4.—Section through 6·5 mm. tadpole, showing position of subintestinal vein on left of gut. Section taken at level Y–Y in text-figure 1, A. × 54.

PLATE VI.

Fig. 1.—Section through 7 mm. tadpole, showing positions of omphalomesenteric, hepatic and lateral veins. × 54.

Fig. 2.—Section through 7 mm. tadpole, showing position of subintestinal vein on ventral surface of gut, also the median postcardinals and Wolffian ducts. × 54.

Fig. 3.—Section through 8 mm. tadpole, showing position of subintestinal vein on right of duodenum, also the main portal vein. Section taken at level X–X in text-figure 1, B. × 54.

Fig. 4.—Section through 9 mm. tadpole, at level of vagus ganglion, showing posterior cerebral vein (two sections combined). × 110.

PLATE VII.

Fig. 1.—Section through 10 mm. tadpole, at level of right median cerebral vein. Showing also the positions of venae jugularis externa and muscularis abdominis. × 54.

Fig. 2.—Section through 24 mm. tadpole, showing positions of subintestinal, gastric and main portal veins, also the posterior vena cava and the ducts of Cuvier. Section taken at level X–X in Plate II, A, and text-figure 1, C. × 24.

ABBREVIATIONS.

Abd, abdominal vein; ac, anterior cardinal vein; acm, arteria coeliacomesenterica; aff, afferent renal veins; agas, anterior gastric vein; anast, dorsal anastomosis round gut; aud, auditory sac; audc, auditory capsule; avc, anterior vena cava.

Bd, bile duct; bp, basal plate; br 1–3, branchial arches 1–3; bra, branchial artery; brac, brachial vein; brv, branchial vein.

Cap, capillary network; caud, caudal vein; cer, ceratohyal; comm, commissural vessels between abdominal and caudal veins; conn, anterior connexion between v. capitis medialis and v. capitis lateralis; cut, cutaneous vein (v. cutanea magna).

Da, dorsal aorta; dC, duct of Cuvier; dmab, dorsal root of v. muscularis abdominis; duod, duodenum.

Eff, efferent renal veins; ej, external jugular vein; eja, ejb and ejc, branches of external jugular vein from branchial arches 1 + 2, 3, and 4 respectively; ejth, branch of external jugular vein from thyroid gland.

Fac, v. facialis; fc, v. facialis communis; fem, v. femoralis; fs, v. facialis superficialis.

Gas, gastric vein; gasd, gastroduodenal vein; gb, gall bladder; glat, lateralis ganglion; gpr, ganglion prooticum; g v, g vii and g x, ganglia of cranial nerves v, vii and x.

H, heart; hb I and hb II, hypobranchials I and II; hep, hepatic vein; hy vii, nervus hyomandibularis vii.

Ic, internal carotid artery; ij, internal jugular vein; int, intestine; ir, interrenal vein; isch, ischiadic vein.

La, lung anlage; lar, larynx; lat, lateralis nerve; latv, lateral vein; ling, v. lingualis; liv, liver (or liver anlage in Plate V); lj, lower jaw; lpc, lateral postcardinal; ly, lymph duct.

Mab, muscularis abdominis vein; mand v, nervus mandibularis v; mcb, musculus constrictor branchialis; mcer, median cerebral vein; mdl, musculus dilatator laryngis; mes, mesonephros; mess, mesonephric sinus; mi, vena mandibularis interna; mp, main portal vein; mpc, median postcardinal vein; mrc, musculus rectus cervicis; msr ii, musculus subarcualis rectus ii; mth, musculo-thyroid vein; mtv, muscle probably corresponding to musculus transversus ventralis iv (Paterson, 1939); my, myotome.

Not, notochord.

Oml, left omphalomesenteric vein; omr, right omphalomesenteric vein; on, vena orbitonasalis; op, opercular vein; oph, vena ophthalmica; opv, nervus ophthalmicus profundus v.

Pal vii, nervus palatinus vii; pan, pancreas; pcer, posterior cerebral vein; ph, pharynx; phar, pharyngeal vein (adult); phv, pharyngeal vein (larva); pron, pronephros; prs, pronephric sinus; pul, pulmonary vein; pula, pulmonary artery; pvc, posterior vena cava.

Raa, ramus abdominalis anterior (anterior anastomosis); rap, ramus abdominalis posterior (posterior anastomosis); rc, ramus communicans; rect, rectum; rp, renal portal vein.

Seg, Wolffian duct; som, somatic veins; st, stomach; sub, subintestinal vein; subc, subclavian vein; sv, sinus venosus.

Th, thymus gland; thh, thyrohyal; thyr, vena thyroidea; ts, truncus supraorbitalis.

Vel, vena capitis lateralis; vcm, v. capitis medialis; vcmd, dorsal element of v. capitis medialis (=vena cerebralis anterior); vcmv, ventral element of v. capitis medialis (=v. orbitonasalis); vmab, ventral root of v. muscularis abdominis.

A RECORD OF SOME WIND-FACETED STONES FROM ROBBERG, PLETTENBERG'S BAY, C.P.

By Lester C. King, D.Sc.

(Read March 19, 1947.)

Following certain studies upon wind-faceted stones in Marlborough, New Zealand,[1, 2] I have long wished to make further studies, including such topics as the distribution of minor facets, undercutting of lower edges and so forth, upon the abundant material in the Namib desert. Such has not yet been my good fortune; but Professor M. S. Taljaard, of Stellenbosch University, was good enough to draw my attention to the specimens recorded at Robberg, Plettenberg's Bay, by Mr. P. J. Rossouw.[3]

These I examined during a brief visit to Robberg in January 1946, and though the results, for reasons set forth, are much less conclusive than I could have wished, certain facts and conclusions are submitted in the belief that they will be useful for correlation with other occurrences at a later date.

The Situation.—The wind-faceted stones, or ventifacts, of Robberg occur in a typical situation littered upon the sand of the southern (seaward) side where it is whipped by winds from the Indian Ocean. There is a funnel-like gully up which these winds pass, and in a hollow towards the base, the logical spot, these stones are found. So situated are they that the south-west is the only effective wind for the cutting of facets; and this must blow often, and with extreme violence.

To my great dismay, I found not only ventifacts but also implements formed by at least five, and possibly six races of man: two Stellenbosch, Middle Stone Age, Strandlooper, and Modern Man. It would thus be unwise to base any far-reaching conclusions upon this assemblage of ventifacts—they have probably been disturbed far too often by wandering feet

[1] Wind-faceted Stones from Marlborough, New Zealand. Journ. Geol., vol. xliv, pp. 201–213, 1936.

[2] On Wind-faceted Stones from the Marlborough Strand-Plain. Trans. Roy. Soc., N.Z., vol. lxvi, pp. 275–280, 1936.

[3] Trans. Geol. Soc. S.A., vol. xxxvi, pp. 69–72, 1933.

to be in exactly their original positions. In the census taken, the most scrupulous care was exercised to exclude any stones which, to such experience as my eye has gained, appeared to have been recently disturbed. It is likely that, despite all precaution, some such have crept into the enumeration, but their number, as shown by the facet directions in the tables themselves, is probably less than ten.

The Material.—A few specimens were originally angular fragments of Table Mountain Sandstone, but the great majority were formed from rounded or broken sandstone pebbles from the Cretaceous Enon conglomerate, which here overlies the solid, Devonian sandstone twenty to thirty feet above sea-level. The material is hard and must have taken a long time to abrade into the typical dreikanter and pyramid forms so abundantly displayed.

Of the mode of development of facets upon originally angular and originally rounded materials I have treated in two former papers[1, 2] to which the reader is referred (see p. 101).

The Census.—A census was taken of all the faceted stones which, upon strict examination, showed no evidence of having been moved at some stage during the development of facets. It comprehended 172 specimens, which bore upon them a total of 347 facets—closely an average of two apiece.

Each specimen had recorded (1) its greatest diameter, (2) the facets and their directions, (3) the relative size of facets, whether *major* or *minor*—*on the same pebble.*

The question of what constitutes major and minor facets, whether *absolute* size or, as here employed, *relative* size is one for future discussion. The former definition has obvious advantages, but is subject to the final disadvantage that, after all, the ultimate size of facets is governed by the size of the stone upon which they exist.

Tables of Results.—The following two tables (p. 103) express concisely the results of the enumeration, and bring out strongly the orientation of most facets at right angles to the south-west or west-south-west wind. The normal supplementary direction north-east to east-north-east is, on the contrary, relatively suppressed, perhaps because the stones lie upon an uphill slope in that direction, which may suppress the eddy current of air usually responsible for the cutting of the rear facet.

Attention may be directed to the small number of minor facets relative to major: 48 to 299 or 1 to 6. This may be due to long-continued abrasion, or to absence of winds or ground currents of air at angles with the main south-west direction. It suggests that the original material did not bear numerous faces, *i.e.* that it consisted of rounded pebbles from the Enon conglomerate.

The occurrence was unsuitable for a study of the relation of minor facets to change in direction of ground air-currents due to adjacent large boulders which I had desired to undertake.

TABLE I.

Relations of Number of Facets to Size of Pebbles.

Greatest Length Main Axis about	1 Facet	2 Facets	3 Facets	4 Facets	5 Facets	6 Facets	Number of Specimens
1″	1	3	1	1	..	..	6
2″	12	24	8	3	1	..	48
3″	15	33	7	2	..	..	57
4″	15	15	5	4	..	..	39
5″	4	5	2	1	1	..	13
6″	4	..	2	..	..	..	6
>6″	2	..	..	..	1	..	3
Total specimens	53	80	25	11	3	..	172 Grand total of specimens

Total of Facets 347
Average Facets per Specimen 2

TABLE II.

Total Facets in Compass Directions.

Major Facets N.	N.E.	E.	S.E.	S.	S.W.	W.	N.W.	Totals
14	31	39	31	25	60	55	44	299
Minor Facets 4	7	3	10	5	11	4	4	48
Totals 18	38	42	41	30	71	59	48	347

Appendix.—For the information of other workers who may undertake similar studies, the data jotted in a ruled notebook *while the stone is in its original position on the ground* are as follows: number, size, petrological nature, directions and relative proportions of facets, and remarks.

For example:

83	$6'' \times 2''$ T.M.S.	N.E., S.E., S.W.	Bears large original cleavage on W. Base tilted N.E. 10° from horizontal.
201	$2'' \times 1''$ Igneous S., S.E., E., N., N.W.		Pyramid, sheltered under lee of large boulder which deflects ground air currents chiefly to S. and S.E.

Above all, as complete an enumeration as possible should be made. An area of 110 sq. ft. in which I once worked had 322 wind-faceted stones.

MICROCYSTIS TOXICA SP. NOV.: A POISONOUS ALGA FROM THE TRANSVAAL AND ORANGE FREE STATE.

By Edith L. Stephens, Botanical Department, University of Cape Town.

(With Plate VIII and two Text-figures.)

(Read May 16, 1945.)

This alga first came into notice after the building of the great dam known as "Vaaldam" across the Vaal River, about 50 miles south of Johannesburg. Vaaldam is a long winding drowned valley, 75 miles long, 15 miles wide at its broadest point, and with a capacity of 220 thousand million gallons. It was completed in 1938, and as it filled it submerged farm-lands which had stretched along the river valley. Perhaps as a result of organic enrichment through the flooding of all this fertile farm-land, and the submergence of many trees and shrubs, there appeared a vigorous "water-bloom" of this alga that by the end of 1942 had extended through 98 per cent. of the whole length and breadth of the dam. The exact date at which it first appeared is unknown, but stock were dying along the banks by December 1940. Losses during the following two years became so severe that Dr. Douw G. Steyn, then Head of the Department of Pharmacology and Toxicology, Onderstepoort Laboratories, and at present Professor of Pharmacology, University of Pretoria, was sent to investigate. Observations on the spot, and experiments in controlled feeding of the fresh living alga to animals at Onderstepoort, put it beyond doubt that the death of the animals was due to its presence in the Vaaldam water they drank. A similar water-bloom of this alga in Bon Accord Dam, close to Onderstepoort, gave exactly the same results with experimental feeding.

This has furnished a clue to mysterious deaths of various kinds of animals which have occurred in the past round pans in the Transvaal and Orange Free State. (A "pan" is a shallow sheet of water ranging in size from a large pond to a small lake.) Some pans have acquired a bad reputation among farmers as somehow causing illness among stock, and the presence of this alga is the probable explanation of many cases of "pan sickness". It seems to be widespread in the south-eastern Transvaal and north-eastern

Free State, but so far is not recorded outside these two Provinces. (A tentative record for Maritzburg Bird Sanctuary proves on re-examination to have been an unusual form of *M. aeruginosa*.)

Dr. Steyn informs me that thousands of cattle and sheep died along Vaaldam, and in his opinion many other animals (horses, mules, donkeys, dogs, hares, poultry, and water-birds) found dead near by were killed by the alga. Dead fish were also found in the dam. When he visited it early in 1943 the water looked "like green pea-soup" with the suspended alga, which he found right down to 40 feet (the lowest depth tested); and masses of it were floating at the surface. The least wind would drive these floating masses to the edge of the dam, where drinking animals might take in so much as to cause their death within a few hours. Treatment with copper sulphate throughout the dam proved successful, and it is now applied as necessary along the marginal shallows with a power-pump from a motor-barge; this keeps the alga sufficiently in check for safety to drinking animals without having to treat the whole mass of water.

This interesting occurrence has given the Onderstepoort laboratories an opportunity to study in detail a case of algal poisoning, and Dr. Steyn is preparing a full report for the Onderstepoort Journal of Veterinary Science. Such cases are very rare, for the algae are a harmless group with only a half-dozen suspects. One is a brown flagellate of brackish water (*Prymnesium parvum* Carter); the others belong to the same Blue-Green class as *Microcystis toxica*. Confirmatory feeding experiments have been carried out only with the flagellate in Denmark (Otterstrøm and Nielsen, 1939) and with *Microcystis flos-aquae* (Wittrock) Kirchner in Minnesota (Fitch, etc., 1934), and in both cases the symptoms produced were quite different from those caused by *M. toxica*. In apparent poisoning by *Gloeotrichia pisum* (Ag.) Thuret, the only other case where symptoms have been described (Arthur, 1883, as "*Rivularia fluitans* Cohn"), these again were different. The living alga is toxic in these species, but in *Aphanizomenon flos-aqua* (L.) Ralfs the poison (in this case hydroxylamine) is a decomposition product of decay (Prescott, 1948).

Pending the publication of Dr. Steyn's paper, those interested in the toxicological and veterinary aspects of poisoning by *M. toxica* will find a useful summary in a pamphlet written by him (Steyn, 1945) for farmers. Only a few of the data he has established concern us here. He has shown that the living alga contains one of the most potent and destructive liver poisons known. Dried material is much less toxic than fresh. If the alga dies in water, the poison diffuses out into the water and there seems to break down, for the water loses its toxicity within a few days. The degree of severity of poisoning varies with the amount of alga taken in: rapid death may follow a large dose, but with quite small quantities, such as

would be taken in by daily drinking at a mildly infected pan, the only outward sign may be a falling-off in condition. Photosensitivity is often marked, and animals suffering from chronic poisoning need to be kept in the shade.

Samples of this alga were sent me by Dr. Steyn, and as it could not be exactly fitted into any described species, I paid a brief visit to the Transvaal in April 1945 to see it living. Material was collected from Vaaldam, from Bon Accord Dam, and from Spaarwater Mine Dam and pans in its neighbourhood. In Vaaldam the alga was present in fair amount, though only visible at the surface along the windward margin, and in the Vaal River it was found right down to Vereeniging; below that I have not collected, but there is evident danger of its being carried down into the Orange River. Comparison with *Microcystis aeruginosa* Kutz., the alga most like it, from an opportune water-bloom in Zeekoe Vlei and Ronde Vlei (small lakes on the Cape Flats), led to the conclusion that it was a distinct though closely allied species, and in view of its poisonous nature *M. toxica* seemed an appropriate name.

Microcystis toxica sp. nov.

Colonia primo solida et homogeneosa, forma diversa; deinde ab divisione rapido cellularum productae sunt in coloniae corpore cellulae confertae in forma filarum vel globarum; filae et globi plerumque in reticulo inaequale cohaerent; colonia simul saccata vel excavata vel spongiformis fit, et perforata inter reticulum; ultimo in filas et globos soluta est. Coloniae in longitudine vel diametro 0·35 mm. ad 2·5 mm.; cellulae in magnitudine structuraque ad *M. aeruginosam* accedent. Species animalibus toxica.

A *M. aeruginosa* praecipue differt reticulo filarum globarumque, et quia venenata est.

Colonies variously shaped and at first solid and composed of numerous cells in a colourless gelatinous investment, later becoming hollow, concave, or spongiform; cells spherical, with 3 to 8 pseudovacuoles, 3·4 μ to 7 μ in diameter, resembling those of *M. aeruginosa*. Multiplication of colonies typically initiated by rapid cell-division localised in streaks or spots, leading to the formation of strands and balls of more or less closely packed cells, the strands variously shaped and loosely united with each other and the balls to form an irregular network. Colony simultaneously expanding and becoming either internally hollowed to form a sac, or else more or less concave, or sometimes spongiform; in expansion becoming irregularly and often brokenly reticulate owing to the disruption of the layers between the strands of the network. Fully developed colonies from 0·3 mm. up to 2·5 mm. in length or diameter, mostly between 0·7 mm. and 1·2 mm. Colony

ultimately falling apart into portions, thence into the component strands and balls, which develop into new colonies. Species toxic, causing disease and death in animals.

Differs from *M. aeruginosa* by the majority of its colonies becoming hollow, by the formation of these strands and balls of closely packed cells connected into a network, by the larger size of its colonies, by its toxicity, and by the odour and colour developed (as described below) in decay.

As in *M. aeruginosa*, the colony begins as a group of similar cells, uniformly distributed in a mucilaginous investment (text-fig. 1, A). It may be rounded, oblong, or irregular in form, and at this stage may divide

A B

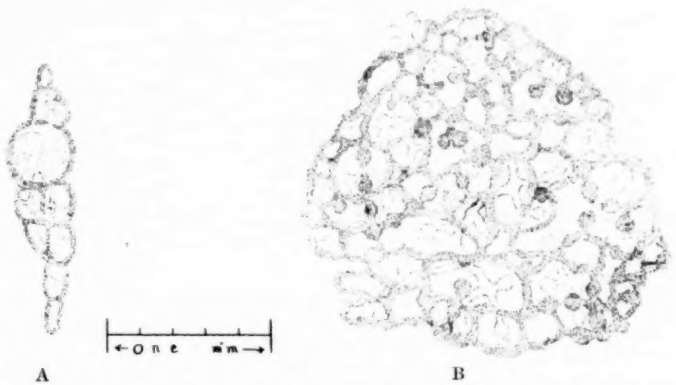
TEXT-FIG. 1.—Drawn from colonies mounted in indian ink to show up the boundary of the mucilage, which is indicated by the broken lines. A. Very young colony. ×300. B. Part of a strand from a mature colony. ×60.

by merely splitting into two. But its usual and typical method of multiplication is quite different, and is only seen as the colony grows in size. It is initiated by the appearance of streaks and spots of more crowded cells, formed by rapid cell-division, in its peripheral part. About the same time, or earlier, the colony may begin to hollow internally so as ultimately to form a sac, which may be closed, or open at one or both ends. Less often it does not become hollowed but more or less concave to a saucer or basin shape, or it may be spongiform, or rarely flattened.

In the streaks and spots, cell-division is so rapid that they become strands and balls of cells more closely packed than the rest of the colony. Sometimes these cells are not much more crowded than the rest, but usually they are much more closely packed, so that the strands often look almost solid in contrast with the rest of the colony. They vary greatly in shape (*cf.* Pl. VIII), most often suggesting bones covered by soft velvet. The balls are round or oval (Pl. VIII, fig. 1), and often form short necklace-like rows Strands and balls join to form a kind of irregularly latticed framework or "skeleton" to the colony. When this is mature, it is usually still possible to distinguish most of the original strands and balls, but they may also become so merged as to give the effect of an almost uniform structure to this network. As it develops and expands, the remainder of the colony, consisting of the non-dividing cells, thins out and ultimately breaks away and disappears in most or all of the interstices. Some of its cells, in their

mucilage, however remain as a minute soft coating to the strands, and as "hinges" at their points of contact. The mucilaginous investment may hollow along with the rest of the colony, and it may also disappear from the interstices of the larger meshes of the network, whose strands then have an individual mucilaginous investment (text-fig. 1, B). But it may also continue to occupy part or all of the interior of the colony even when that is mature, especially in the smaller colonies.

A mature colony is usually made up of both strands and balls, but may be composed entirely of one or the other. The framework they form may be quite a neat hollow network, as in text-fig. 2, B, or most fantastic. The



TEXT-FIG. 2.—Mature colonies, medium-sized and large. ×25. Each dot is a cell of the colony. For clearness, the network has been drawn only one cell-layer thick, while the strands of the lower surface are shown in outline only, and in B a few of them have been omitted.

illustrations will give an idea of their protean variety of structure. These fully developed colonies often look as though the skeleton of some small animal had been dissociated and the bones then joined in a kind of fancy basket-work.

The fully formed network ultimately breaks up; first into portions often reminiscent of the cuneiform colonies of *M. scripta* (Rich.) Lemm. (*cf.* Pl. VIII, fig. 3), and then these fall apart at the "hinges" into the constituent strands and balls. Much of the material thus resembles skeletal fragments and jumbled bones. As far as one can follow from preserved material, the balls seem ultimately to develop into rounded or oval colonies, the strands into ones of more varied and fantastic shape.

The measurements given above have been taken from material in full pans and dams, and should not be applied as a criterion where conditions

are unfavourable for normal growth. For example, the large hollow known as "Sandpits", to the N.E. of Spaarwater Mine, contained a pan in which *M. toxica* was flourishing full size, and also a shallow muddy depression with water less than ankle-deep, in which it was dwarfed to less than half normal size. In good conditions, the average size of the colonies is about 1 mm.

In colour it is about the same lettuce-green as *M. aeruginosa*, deepening to spinach-green a foot or more below the surface. Both species dry to a verdigris coating on stones.

Points of difference between this species and the closely allied *M. aeruginosa* are as follows:—

(1) Hollow colonies with peripherally arranged cells, the commonest type here, are very rare in that species, which typically forms a solid, clathrate, or sponge-like colony. The Russian forma *sphaerodictyoides* Elenk. is an exception, for it has hollow nets. But in the description (Elenkin, 1938, pp. 106–109) no mention is made of strands and balls of close-packed cells such as characterise *M. toxica*, nor are any shown in the figure (Elenkin, fig. 29); so in spite of a superficial resemblance it would seem unlikely that the two are identical.

(2) *M. aeruginosa* does not develop any framework of close-packed cells. It is true that there appear quite often in its colonies points of rapid division, resulting in groups of rather close-packed cells, the colony then breaking up into portions each with a group as nucleus. But these groups never join to form the clear-cut reticulum which usually characterises *M. toxica*, in contrast with the comparatively soft and vague outlines of *M. aeruginosa*.

(3) The average size of *M. aeruginosa*, measured in a large number of colonies from the Zeekoe Vlei bloom and also from published figures, is about half a millimetre, *i.e.* half the average for *M. toxica*. The largest colony was just under a millimetre; compare with the 2·5 mm. attained by *M. toxica*.

(4) The poisonous nature of *M. toxica* has been fully proved, whereas *M. aeruginosa*, most widespread and frequent cause of "water-bloom", has never been suspect. A dairy farmer on the shores of Ronde Vlei tells me that his cattle have shown no ill-effects from the quite large doses they must have drunk during the 1946 bloom.

(5) Dying and decomposing material of the two species shows marked differences. Dr. Steyn (Steyn, 1945) described *M. toxica*, wind-driven in masses into the creeks of Vaaldam, as decaying with a "most obnoxious stench", detectable at a considerable distance, and as showing a remarkable

play of colours from green through blue to purple, with a red fluorescent liquid in the cracks of the decaying mass. Decaying *M. aeruginosa*, on the other hand, forms only a milky-white scum, which may be stalely ill-smelling if in quantity, but with nothing like the foul "dead animal" odour that I noticed from almost dry pools coated with dying and decaying *M. toxica*.

As I have not succeeded in growing *M. toxica* in culture, this work has had to be done almost entirely on preserved material. There are many points which need further investigation on living material and in the field, and it is hoped that this preliminary study will be amplified and corrected by some worker in its home on the Highveld.

For the collecting apparatus used in this investigation I have to thank the Carnegie Corporation, as it was originally procured with a grant made from their funds through the Research Grant Board of South Africa. I am much indebted to Dr. Dyer, Miss Weintroub, Mrs. Moss, and other Transvaal botanists who kindly helped me to collect material; to Miss Bottomley of the Cryptogamic Laboratory of the Division of Botany at Pretoria, who allowed me the use of the Laboratory to examine and fix it; to Mr. Talbot of that Laboratory, who while at Kew helped with literature unobtainable here; to Dr. M. A. Pocock and Mr. Talbot for taking the microphotographs; and especially to Dr. Steyn, who introduced me to this interesting alga and has furnished much of the information here given.

SUMMARY.

Microcystis toxica Stephens (sp. nov.) is a poisonous blue-green alga apparently endemic to South Africa. As a "water-bloom" in the Vaaldam, Transvaal, it has killed thousands of cattle and other animals. The colonies average 1 mm. in diameter, and when mature usually consist of a peripheral network of strands and balls of close-packed cells in a mucilaginous investment. It differs from *M. aeruginosa* by its larger size, peripheral network of cells, toxicity, and odour and colour in decay.

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[*Photo, P. H. B. Talbot.*

FIG. 1.—Dissection of part of a large colony, to show balls of cells forming. ×120.

[*Photo, M. A. Pocock.*

FIG. 2.—Two smaller colonies, younger on left, showing how the cells of the strands and balls become closer packed as the colony matures. ×120.

[*Photo, M. A. Pocock.*

FIG. 3.—Maturing, mature, and disintegrating colonies. ×25. A and G are the youngest; G is forming balls of cells. In D and F most of the cells in the meshes of the network are still in place, hence their comparative opacity. B, C, and E are the only other unbroken colonies. The remainder have already begun to fall apart, or are fragments.

Growth forms of *Microcystis toxica* Stephens.

Edith L. Stephens. *Neill & Co., Ltd.*

VARIATION IN THE PHYTOPLANKTON OF TABLE BAY. OCTOBER 1934 TO OCTOBER 1935.

With a Note on

THE CALORIFIC VALUE OF *CHAETOCEROS* SPP.

By W. J. and L. D. Copenhagen.

(With two Text-figures.)

(Read October 16, 1935.)

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1. Introduction.

The first observation on plankton in the South African seas was made by Captain James Cook, R.N., F.R.S. In his Journal he records:

> ". . . weighed from Table Bay on November 30th, 1776, though it was not until December 3rd that we got clear of the land. On the 6th, the ships passed through several spots of water nearby of a red colour. When some of this was taken up, it was found to contain a large quantity of small animals of a reddish hue and which the microscope discovered to resemble crayfish".

Since Captain Cook's time many ships have taken samples of plankton from the coastal and neighbouring seas. Among these must be mentioned H.M.S. "Challenger", "Valdivia", "Meteor", "Dana", "Discovery I", "William Scoresby" and "Discovery II". The results of the findings of these plankton samples are embodied in the respective reports of the expeditions concerned.

Under the directorship of the late Dr. J. D. F. Gilchrist (Government Marine Biologist, 1895–1928) of the Union of South Africa, the S.S. "Pieter Faure" collected samples of plankton from the South African coastal seas, and the results were published by Cleve in 1904 and 1908. These deal with zooplankton.

Various samples of plankton were examined and identified from time to time, but it was not until October 1934 that a systematic count of phytoplankton of Table Bay was made, the aims being to investigate—

(1) The seasonal variation in the plankton, both qualitatively and quantitatively.
(2) Changes to the physical environment.

Prior to October 1934, occasional zooplankton counts were made by Dr. Barnard of the South African Museum, and odd samples of phytoplankton were identified by the late Mr. E. J. Steer, a very keen diatom enthusiast.

2. Stations and Methods.

The geographical position of the Cape Peninsula is unique owing to the fact that it occupies the south-western extremity of the African Continent. The waters of Table Bay are subjected to the influences of the Atlantic, Antarctic and Indian Oceans.

The scope of the investigation was necessarily restricted by the amount of time that it was possible for us to devote to it, apart from other routine work. Collection was concentrated along a three-mile line sufficiently far from Cape Town to be free from harbour pollution, industrial wastes and estuarine influence (see fig. 1). Efforts were made to reach this line every week-end in a yacht. Plankton collections and water samples were taken from the surface layers only. The eight-metre racing yacht "Erica" did not prove an ideal type of craft for this work in the unsheltered waters of Table Bay. Thus during periods of inclement weather, the Government Police launch and Harbour tugs assisted in maintaining the regularity of sampling.

Weather records were kept, and the plankton and water samples were examined within twenty-four hours of collection.

Quantitative estimations of the phytoplankton were carried out with an apparatus described in detail by the writer (1) in a previous communication. This enables one to obtain comparable values (in arbitrary colour units) of the phytoplankton in a cubic metre of sea-water. As this apparatus is designed for towing and not for vertical hauls, the results are not comparable with those obtained by Harvey (2), the originator of the method, in the English Channel. Towing just beneath the surface, our apparatus

is nearly always fishing at about the optimum level for diatom growth, whereas a vertical haul covers the whole of the euphotic layer. The very

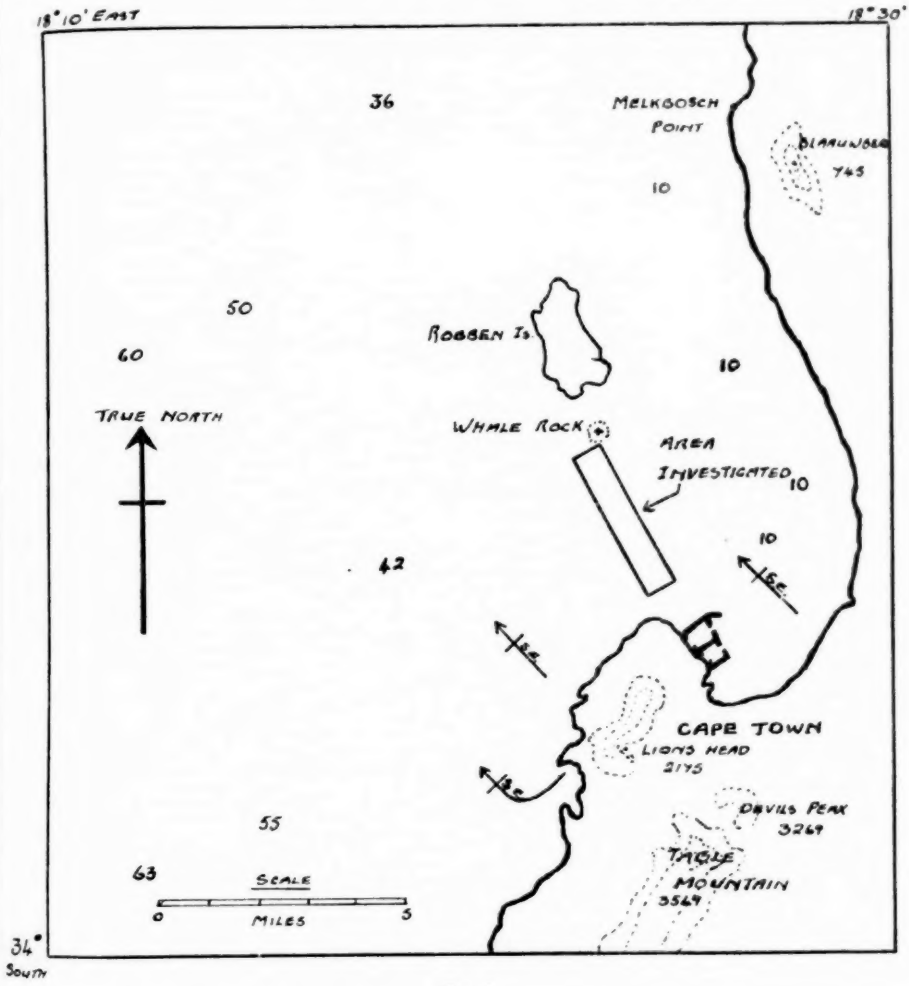

FIG. 1.

high values obtained by this method are probably to be attributed to this fact. It would have been quite impossible to carry out a sufficient number of vertical hauls in the time at our disposal, and the method remains

adequate to show up the main features of seasonal variation in quantity, which formed the principal object of the investigation.

The qualitative counts were obtained by examining four fields from each of three wet mounts of the well-mixed sample, and the results were recalculated on a percentage basis as shown in the tables. In coastal plankton with relatively little qualitative variation through the year, this is adequate to show up the dominant species. These qualitative samples were collected by means of a 200-mesh silk half-metre circular plankton net.

3. Phytoplankton.

(a) *General Aspect.*

The general nature of the phytoplankton cycle is shown in fig. 2 with sunshine and surface temperature records for the corresponding period. It will be seen that during the early summer months, production fluctuated violently without ever reaching a very high level. Sunshine had not yet reached its maximum for the year, and over the same period surface temperature also varied widely. This last feature strongly suggests that at this time production was regulated by the waxing and waning of strong winds. A period of calm following upon a strong south-easter would be favourable to production, but further gales would drive the inshore surface water out to sea before the production could proceed to a high level. Hart (3) has shown how important the influence of strong variable winds can be upon the phytoplankton of inshore waters in regions of much higher nutrient salt content.

Over midsummer production was slight, as has been found in almost all temperate latitudes previously investigated. This is probably not due to depletion of the nutrient salts in the surface layers here, however, for the quantity of phytoplankton observed was considerably greater than that found in the English Channel, at the corresponding period. The dominance of *Rhizosolenia* spp. on December 30th suggests that the surface water of the bay was more oceanic in character than usual. The sub-tropical surface water of the open South Atlantic is poorer in nutrient salts, and not so well "seeded" with diatoms as the coastal water. Thus the poor phytoplankton at midsummer may be attributed to a tongue of Agulhas water or a change in the amount of upwelling.

In February, just after the sunshine figures reached their maximum for the year, a much larger period of production occurred, accompanied by a sharp fall in the general level of surface temperature, suggesting the upwelling due to offshore southerly winds had again become the critical factor. *Chaetocerids* predominated at this time, and again during a similar peak period in March–April. These two maxima presumably correspond

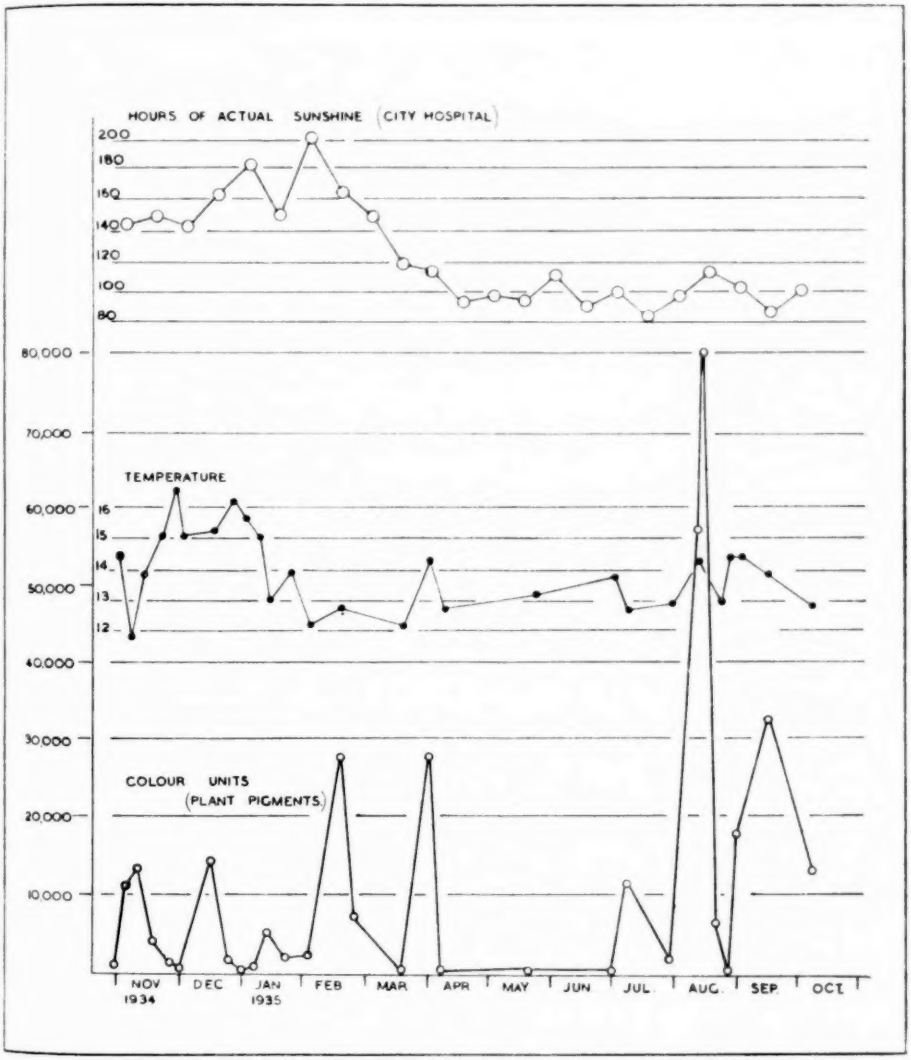
HOURS OF ACTUAL SUNSHINE (CITY HOSPITAL)
200
180
160
140
120
100
80
80,000
70,000
TEMPERATURE
60,000
16
15
14
13
12
50,000
40,000
30,000
COLOUR UNITS
(PLANT PIGMENTS)
20,000
10,000
NOV
1934
DEC
JAN
1935
FEB
MAR
APR
MAY
JUN
JUL.
AUG.
SEP.
OCT.

FIG. 2.

to the usual autumn maximum found in slightly higher temperate latitudes in both hemispheres.

Production was low during the winter months April–July. At this time of year the south-easterly offshore winds are less prevalent, upwelling will be less, and occasional north-westerly gales tend to pile up poorer oceanic water against the coast. As will be seen from the tables, increased proportions of *Rhizosolenia* and *Thalassionema* suggested a more oceanic type of phytoplankton.

The main phytoplankton increase occurred in August, with enormously rich catches, first of *Chaetoceros* with neritic forms such as *Navicula*, secondly with the more oceanic element *Thalassionema* spp. (dominant on August 11th). This coincided with the first rise of sunshine figures above the minimal winter values and sharp increase in surface temperature; wind records on this day indicated west to north-west 8–18 m.p.h. A very sharp fall in the following fortnight, in both temperature and phytoplankton, illustrates yet again the importance of local wind conditions. During this period the wind records reveal that south-easterly offshore winds were predominant.

This drop was accompanied by the only observation of marked predominance of holozoic organisms (*Tintinnus*) in the microplankton. Evidently the surface water present in Table Bay on August 25th was of very different origin from that sampled on August 11th. In September, a further large increase of similar type suggests that the main increase of early spring had merely been interrupted by the violent short-period changes in local conditions which are such a feature of the area investigated.

From the quantitative phytoplankton tables it will be seen that *Chaetoceros* spp. were the most important members of the planktonic vegetation. Of these, *Chaetoceros sociale* was the most prominent, and should probably be regarded as a neritic species in southern sub-tropical waters. Other species such as *C. decipiens* and *C. furca* are sometimes numerous in oceanic water, but tend to be far more abundant and show stronger growth of the individual frustules in coastal waters (Hart, personal communication).

Other forms occurring in large quantities comprised *Melosira* and *Navicula* of the definitely neritic element. (Mr. R. Charter has found that the dominant *copepod* spp. are also neritic forms—R. Charter, unpublished data.)

Rhizosolenia spp. (mostly a thin phase of *R. alata*) and *Thalassionema logissima* among more oceanic species. The relatively high importance of *Coscinodiscus* spp. in late winter seems a very general feature of the behaviour of this genus throughout the world wherever the phytoplankton cycle has been studied over a period of a year.

Doubtless *Coscinodiscus* spp. are actually more abundant at other

times, but then their numbers are insignificant compared with those of other species. In winter the other forms, showing greater seasonal variation, become less important, and the frequency with which *Coscinodiscus* spp. have been recorded among the food of plankton animals is doubtless due in some measure to the relatively small range of seasonal variation in abundance of that genus.

(b) *Conclusions.*

It has been shown that a rich phytoplankton development occurs in Table Bay in early spring, followed by smaller maxima in early summer and autumn. *Chaetoceros* spp. and neritic forms predominate, and it is probable that production as observed is quite local. Violent short-period fluctuations are probably explicable on the grounds of rapid changes in the water-masses caused mainly by upwelling due to local wind conditions. In general, however, the main periods of production show striking agreement with those shown in the smoothed curve published by Dakin (4) of the production in Sydney Harbour, N.S.W.

Owing to unavoidable limitations in the methods adopted, it is not yet possible to compare the richness of the Cape waters directly with those of other seas, but it is probable that at times the production equals or exceeds anything known from other temperate localities.

4. Quantitative Phytoplankton Tables.

23.10.34.	
Chaetoceros socialis / *Chaetoceros* spp.	90 per cent.
Thalassionema sp. / *Rhizosolenia* sp.	10 ,,
30.12.34.	
Rhizosolenia sp.	48 per cent.
Chaetoceros spp.	26 ,,
Thalassionema sp.	10 ,,
Coscinodiscus sp.	8 ,,
Navicula sp.	4 ,,
Tintinnus sp.	4 ,,
17.2.35.	
Chaetoceros spp.	90·4 per cent.
Thalassiosira sp.	5·7 ,,
Nitzschia seriata	1·8 ,,
Thalassionema nitzschoides	0·9 ,,
Stephanopyxis tunis	0·5 ,,
Coscinodiscus sp.	0·3 ,,
Rhizosolenia alata	0·1 ,,
Peridinium sp.	0·3 ,,
17.3.35.	
Chaetoceros spp.	84·9 per cent.
Thalassionema sp.	3·4 ,,
Melosira sp.	3·1 ,,
Biddulphia sp.	3·1 ,,
Navicula sp.	1·5 per cent.
Coscinodiscus sp.	1·3 ,,
Peridinium divergens	1·3 ,,
Rhizosolenia sp.	1·0 ,,
Thalassiosira sp.	0·5 ,,
Chaetoceros socialis present.	
14.4.35.	
Rhizosolenia sp.	34·2 per cent.
Thalassionema sp.	26·3 ,,
Peridinium divergens	26·3 ,,
Chaetoceros sp.	17·1 ,,
Coscinodiscus sp.	9·2 ,,
Ceratium furca	4·0 ,,
Tintinnus sp.	2·6 ,,
Radiolarians sp.	2·6 ,,
Navicula sp.	1·3 ,,
30.6.35.	
Chaetoceros spp.	68·5 per cent.
Thalassionema sp.	14·7 ,,
Coscinodiscus sp.	5·9 ,,
Radiolaria	4·3 ,,
Rhizosolenia sp.	3·1 ,,
Biddulphia sp.	2·9 ,,
Planktoniella sol.	0·4 ,,
Ceratium tripos	0·1 ,,
Formanifera	0·1 ,,

28.7.35.

Coscinodiscus sp.	33·2 per cent.
Thalassionema sp.	19·1 ,,
Navicula sp.	14·6 ,,
Chaetoceros spp.	11·4 ,,
Melosira sp.	6·7 ,,
Ceratium tripos	4·6 ,,
Ceratium furca	2·8 ,,
Biddulphia sp.	2·8 ,,
Rhizosolenia sp.	1·9 ,,
Tintinnus sp.	1·4 ,,
Peridinium divergens	0·5 ,,
Radiolaria	0·5 ,,
Planktoniella sol.	0·5 ,,

5.8.35.

Chaetoceros spp.	46·7 per cent.
Navicula sp.	14·2 ,,
Coscinodiscus sp.	11·0 ,,
Thalassionema sp.	7·9 ,,
Melosira sp.	7·4 ,,
Biddulphia sp.	5·4 ,,
Radiolaria	2·3 ,,
Thalassiosira sp.	2·3 ,,
Rhizosolenia sp.	0·8 ,,
Ceratium tripos	0·8 ,,
Planktoniella sol.	0·5 ,,
Tintinnus sp.	0·2 ,,
Ditylium brightwelli	0·2 ,,
Peridinium divergens	0·2 ,,

10.8.35.

Thalassionema sp.	64·4 per cent.
Chaetoceros spp.	15·7 ,,
Coscinodiscus sp.	9·1 ,,
Thalassiosira sp.	7·7 ,,
Navicula sp.	1·9 ,,
Melosira sp.	0·8 ,,
Biddulphia sp.	0·2 ,,
Peridinium divergens	0·1 ,,
Ditylium brightwelli	0·1 ,,
Chaetoceros socialis present.	

11.8.35.

Thalassionema sp.	46·5 per cent.
Chaetoceros spp.	32·2 ,,
Coscinodiscus sp.	8·6 ,,
Thallasiosira sp.	5·4 ,,
Navicula sp.	5·1 ,,
Melosira sp.	1·4 ,,
Biddulphia sp.	0·5 ,,
Peridinium divergens	0·2 ,,
Ceratium tripos	0·1 ,,
Chaetoceros socialis present.	

18.8.35.

Tintinnus sp.	44·2 per cent.
Melosira sp.	20·0 ,,
Peridinium divergens	10·7 ,,
Chaetoceros spp.	9·5 ,,
Ceratium furca	6·0 ,,
Thalassionema sp.	4·8 ,,
Coscinodiscus	3·6 ,,
Ceratium tripos	1·2 ,,
Chaetoceros socialis present.	

25.8.35.

Melosira sp.	79·5 per cent.
Coscinodiscus sp.	7·5 ,,
Biddulphia sp.	7·5 ,,
Ceratium tripos	1·9 ,,
Tintinnus	0·9 ,,
Rhizosolenia sp.	0·9 ,,
Peridinium divergens	0·9 ,,
Ceratium furca	0·9 ,,

1.9.35.

Chaetoceros spp.	66·8 per cent.
Melosira sp.	10·9 ,,
Thalassionema sp.	10·7 ,,
Rhizosolenia sp.	4·3 ,,
Coscinodiscus sp.	2·6 ,,
Ceratinum furca	1·2 ,,
Planktoniella sol.	1·0 ,,
Thalassiosira sp.	1·0 ,,
Navicula sp.	0·2 ,,
Tintinnus sp.	0·5 ,,
Peridinium divergens	0·4 ,,
Ceratium tripos	0·2 ,,
Biddulphia sp.	0·2 ,,

15.9.35.

Chaetoceros spp.	64·8 per cent.
Navicula sp.	10·6 ,,
Thalassionema sp.	9·0 ,,
Rhizosolenia sp.	5·6 ,,
Melosira sp.	4·1 ,,
Thalassiosira sp.	3·1 ,,
Coscinodiscus sp.	1·8 ,,
Dinophysis and *Peridinium divergens*, *Planktoniella* sol., *Ceratium furca*	1·0 ,,

6.10.35.

Chaetoceros spp.	64·1 per cent.
Melosira sp.	9·7 ,,
Thalassiosira sp.	5·7 ,,
Thalassionema sp.	5·6 ,,
Navicula sp.	5·5 ,,
Rhizosolenia sp.	3·9 ,,
Coscinodiscus sp.	1·9 ,,
Dinophysis sp.	1·4 ,,
Biddulphia sp.	0·6 ,,
Peridinium divergens	0·4 ,,
Planktoniella sol.	0·2 ,,
Ceratium tripos	0·2 ,,
Radiolaria	0·2 ,,
Chaetoceros socialis present.	

13.10.35.

Chaetoceros spp.	29·6 per cent.
Thalassiosira sp.	21·6 ,,
Navicula sp.	11·0 ,,
Melosira sp.	11·0 ,,
Thalassionema sp.	10·7 ,,
Coscinodiscus sp.	7·0 ,,
Peridinium divergens	3·0 ,,
Rhizosolenia sp.	2·9 ,,
Eucampia sp.	2·0 ,,
Dinophysis sp.	0·5 ,,

Radiolaria	0·3	per cent.	
Planktoniella sol.	0·1	,,	
Ceratium furca	0·1	,,	
Tintinnus sp.	0·1	,,	
10.11.35.			
Chaetoceros spp.	61·6	per cent.	
Thalassiosira sp.	14·2	,,	
Thalassionema sp.	9·8	,,	
Melosira sp.	7·4	per cent.	
Navicula sp.	2·9	,,	
Coscinodiscus sp.	2·3	,,	
Biddulphia sp.	0·6	,,	
Peridinium divergens	0·6	,,	
Dinophysis	0·3	,,	
Ceratium tripos	0·3	,,	
Chaetoceros socialis present.			

5. Calorific Value of *Chaetoceras* spp.

The genus *Chaetoceras* appears to be the main constituent of the phytoplankton in Table Bay. Very dense gelatinous catches have been made from time to time, in which *Chaetoceras socialis* figures prominently. During the morning of February 17th, 1935, using a half-metre plankton net (200-mesh silk), such jelly-like catches were obtained at two points approximately 4 miles apart between the Cape Town Breakwater and Robben Island.

The two samples were mixed, and the dominant phytoplankton were as follows:—

Chaetoceras (*socialis* and *decipiens*)	90·4	per cent.
Thalassiosira	5·7	,,
Nitzschia seriata	1·8	,,
Thallassiothrix nitzschoides	0·9	,,
Stephanopyxis turris	0·5	,,
Coscinodiscus radiatus	0·3	,,
Rhizosolenia alata	0·1	,,
Peridinium sp.	0·3	,,

Direct counts (on dilution) of the mixed sample gave an average figure of 27 million cells per c.c.

The corresponding number of Harvey's "colour units" (average of 4) gave 165 units per c.c. This corresponds to 164,000 cells per "colour unit".

A quantitative device for estimating phytoplankton indicated that over the distance of approximately three miles (see above), running approximately one metre below the surface, the average number of "colour units" per cubic metre of sea-water (*i.e.* between the points where the above half-metre plankton catches were made) was 27,750.

The sample consists entirely of phytoplankton, as no zooplankton were observed.

A small portion of the mixed sample (from the half-metre plankton nets) was now taken for analysis. The following are the results:—

Phytoplankton in its natural state:

Apparent density	0·98	
Water	92·9	per cent.
Dry matter (by difference)	7·1	,,

The remainder of the mixed sample was now filtered through a fine grade of filter-paper on a Buchner funnel. This was dried at 105° C., and fat, protein and ash determined.

Brandt's figures (5) are shown in the second column.

Chemical analysis of the dry material (in percentages):

	Mixed Sample.	Brandt's.	
Fat . . .	2·1 per cent.	2·5 per cent.	
Protein . .	8·1 ,,	10·11 ,,	
Ash (silica, etc.) .	70·7 ,,	64·66 ,,	
Carbohydrates .	19·1 ,,	21·5 ,,	(by difference).

Note.—The somewhat high ash value here is probably due to sea salts from adherent sea-water.

Calorific Value.—A convenient quantity of the dried sample was taken and its calorific value was found to be 1175 calories per gm. (This is the mean value from duplicate samples in a standard type of Mahler-Cook bomb.)

This value appears to be low in comparison with the calculated theoretical calorific value. On the assumption that 1 gm. of fat is equivalent to 9·3 calories, 1 gm. of protein is 5·3 calories, and 1 gm. of carbohydrate equals 4·1 calories, the theoretical value is 1400 calories.

It is suggested that, owing to its high ash content, it is possible that particles of unburnt carbon may be enclosed in the ash. This would account for a lower value.

On the basis of the theoretical value, *i.e.* 1400 calories in the dry material, a product containing 93 per cent. of water would indicate that in phytoplankton catches where *Chaetoceras* is dominant, the calorific value is of the order of 98 calories per gm. or 98 calories (large calories) per kilogram. According to various authorities, the fuel value of water-melon is 132 calories per kilo, celery 154 calories per kilo, and rhubarb 143 calories per kilo. (All these figures are for the vegetables as purchased.)

Cooper (6) has utilised the "colour unit" as a basis with reference to certain constituents of plankton. In a similar manner, in this sample it was found that 1 c.c. of the mixed catch was equivalent to 165 colour units. Furthermore, the average value over approximately 4 miles was 27,750 colour units per cubic metre. This would give an equivalent concentration of plankton whose dry weight is known. In order to make it clear, the calculation is shown in full:

25×165, *i.e.* 4125 colour units = 0·587 gm. dry plankton.

$\therefore$ 7028 colour units = 1 gm. dry plankton, *i.e.* 1400 cals.

$\therefore$ 27,750 colour units = 3·8 ,, ,,

i.e. 5320.

It is therefore shown that 5320 calories are contained in 1 cubic metre of sea-water during this period.

6. Acknowledgments.

We have to thank the South African Research Grant Board for a grant of £10 for the purchase of half-metre plankton net. We also have to thank Dr. T. J. Hart for kindly reading through the original manuscript and giving very valuable advice and recommendations.

We desire to pay a tribute to the late Mr. E. J. Steer and also to Mrs. Steer for their unbounding enthusiasm, assistance and interest in this work, and we desire to place on record that Mr. E. J. Steer was probably the first systematic amateur diatom enthusiast at the Cape.

Our thanks are also due to many members of the Royal Cape Yacht Club who assisted in procuring samples.

Finally, we are grateful to Professor J. Day, of the Zoological Department of the University of Cape Town, for his continued and stimulating interest in this work.

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STUDIES OF SOUTH AFRICAN SEAWEED VEGETATION.

II.—South Coast: Rooi Els to Gansbaai, with Special Reference to Gansbaai.

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(With Plates IX, X, and eight Text-figures.)

(Read November 20, 1946.)

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Introduction.

This is the second of a series of papers dealing with the algal vegetation of the South African coast. The previous paper (Isaac, 1937 *b*) dealt with west coast vegetation influenced by the cold Benguela current. A more general consideration of South African algal vegetation of warm and cold sea waters considered chiefly from a geographical point of view has also been published (Isaac, 1938). In those papers as well as in this, attention has been concentrated chiefly on the character of the seaweed vegetation in relation to sea temperature, although other aspects of seaweed ecology have received attention. The conditions, especially the ocean currents, affecting the temperatures of South African coastal waters have been considered in greater detail in a separate paper (Isaac, 1937 *a*). Attention should also be called to a number of papers by Professor T. A. Stephenson and his co-workers. These are concerned chiefly with animal species, but algae are considered (for references see Stephenson, 1944). Although these papers constitute a considerable body of data, no specific account is included of the coast between Rooi Els and Gansbaai.

Since investigations of marine algal ecology were begun, taxonomic studies on South African marine algae have been undertaken by Papenfuss (1940 *a* and *b*, 1943, 1944), Manza (1937), Levring (1938), and Kylin (1938). These studies, especially those of Papenfuss, have resulted in a number of changes in nomenclature, in the description of new species and in corrections of the authorities cited for various species, as well as in a renaming of material in the Tyson and Becker collections in the Bolus Herbarium, University of Cape Town. In view of this, and because the seaweed flora of South African coasts is not widely known, a list of the species considered has been included and, where necessary, taxonomic notes have been added. This should avoid confusion due to the same species being given different specific names in this and previous papers. No attempt has been made to include all the species observed and collected, but only those species that are dominant, common, fairly common, or of special ecological interest. Plants referred to only by generic name are not included in the list. With less common (or only very locally common) species some personal bias may have been unavoidable in regard to exclusion of the smaller plants. Thus, species of *Bryopsis* and *Ceramium* have not been listed. The most serious omissions probably relate to the Corallinaceae. No identifications of the encrusting species (Melobesieae) are available, and only a few of the commonest Corallineae have been cited and in most cases by generic name only. In this connection we would draw attention to the description of new South African species by Manza (1937, 1940), but it is still not possible to name many of the South African Corallineae.

More detailed investigations were made at Gansbaai, but those made at Hermanus and especially at Rooi Els (fig. 1) were rather in the nature of a reconnaissance. General observations were made at other localities on both sides of the Danger Point Peninsula. A general account is bound to be oversimplified, but the outstanding features and modifications are described. It was not possible to make observations in any one locality at intervals throughout the year, as was done for the west coast at Melkbosch, but the

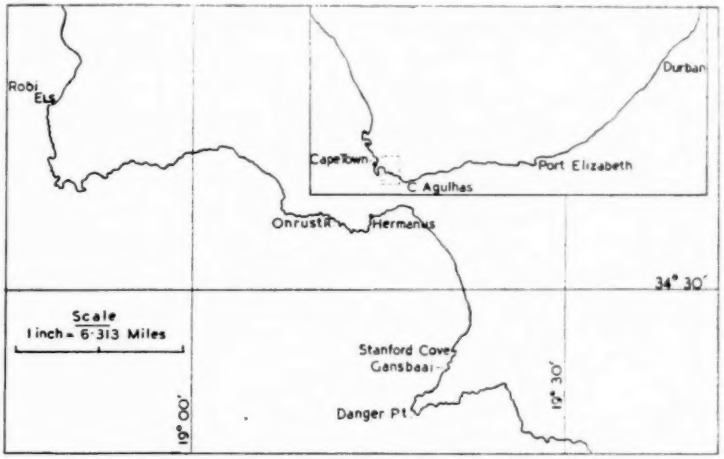

FIG. 1.—Map of the region between Rooi Els and Danger Point. Outline map of the coast-line of South Africa inset.

total set of observations made extends over a considerable part of the year, as shown below:

Gansbaai, January, April, August.
Rooi Els, September, October.
Hermanus (including *Onrust*), March, end of May, early June, July.

Considered in relation to a knowledge of other parts of the coast at different times of the year, these observations taken together make it possible to give an account which is substantially correct for the algal vegetation throughout the year. Careful studies at different seasons are likely to elicit additional interesting facts.

ENVIRONMENTAL CONDITIONS.

Along the greater part of the Union coasts the temperatures of coastal waters are conditioned by ocean currents: the slow-flowing relatively cold

Benguela current along the west coast, and the warm Agulhas current along the east coast and the south coast as far as Cape Agulhas. At any particular locality, of course, the effect of these currents may be considerably modified by local conditions. The coast-line under consideration lies between Cape Agulhas and the southern end of the Cape Peninsula. This region is not directly subjected to the influence of either ocean current, and local variations in conditions are more marked. The contrast in flora and vegetation between Strandfontein on the one hand and Rooi Els on the other is very considerable. This contrast is, however, an extreme one, and no such contrast occurs between the localities dealt with here and, as far as I am aware, for any locality between Rooi Els and Gansbaai.

Although the bulk of the Agulhas current is deflected back eastwards at a higher latitude as the Agulhas return current, smaller branches of the Agulhas stream penetrate to the west of Cape Agulhas. Investigations carried out by the Union Division of Fisheries have resulted in the location of two such branch currents. One of these flows westwards, its waters merging with those of the Atlantic Ocean. The second flows around Cape Agulhas and then along the coast, but at some distance away from it, until, at the latitude of Salhanha, it has become so mixed with Atlantic waters that it can no longer be distinguished. The upwelling cold, less saline water does not reach the surface between Cape Point and Cape Agulhas (von Bonde, 1939).

For the coast between Rooi Els and Gansbaai, sea temperature records are available only for Hermanus. Fortunately records are also available for Danger Point, about five miles distant from Gansbaai. Detailed observations were not made at Danger Point, but general observation showed that the seaweed vegetation was not essentially different from that at Gansbaai. Consequently the records for both Hermanus and Danger Point are considered as relevant in characterising the sea-temperature status of the extent of coast-line under consideration.*

The mean annual surface sea temperature for Hermanus for the three years 1901–1903 is 14·5° C. The corresponding value for Danger Point is 15·5° C.; while for the period 1900–1903 the mean temperature of surface waters at Danger Point is 15·6° C. The mean monthly averages of these two localities for 1901–1903 are shown in fig. 2. The following points may be noted:—

(1) The values for Danger Point are higher than those for Hermanus except in December.

* Data for Hermanus are contained in the Reports of the Government Biologist for 1901, 1902, 1903, and the first half of 1904 (Gilchrist, 1902, 1903, 1904, 1905). Corresponding data for Danger Point are contained in the same reports as well as in that for 1900 (Gilchrist, 1901).

(2) The temperature data for Danger Point are not much higher than those for Hermanus except in March (2·2° C.), and to a lesser extent in January (1·4° C.) and April (1·25° C.).

(3) The seasonal sequence of changes shows the same trends in both localities.

If the values for Hermanus are compared with the mean monthly temperatures of Danger Point for the four years 1900–1903 the comments

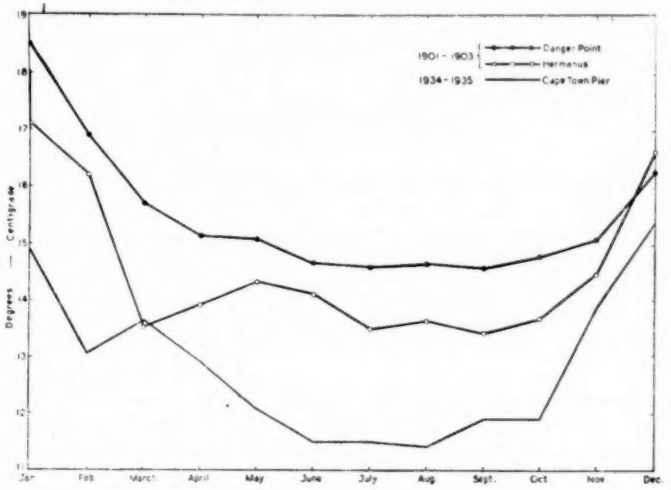

FIG. 2.—Curves showing the monthly mean temperatures at Danger Point, Hermanus, and Cape Town Pier.

made above still apply since the differences in the two sets of values for Danger Point are small.

The difference between the means of the maximum mean monthly temperatures of the two localities for 1901–1903 is only 0·3° C., Danger Point having the higher value. The means of the minimum mean monthly temperatures for the same period are 14·2° C. and 12·8° C. for Danger Point and Hermanus r s pectively—a difference of 1·4° C. These values confirm the somewhat higher general level of temperature throughout the year at Danger Point, which is shown in fig. 2. The mean monthly surface sea temperatures for Cape Town Pier are included in fig. 2 for comparison. The data used are for 1934 and 1935 * since data for 1901–1903 are

* These data were made available by the courtesy of the Manager, Bathing and Seaside Attractions, Cape Town.

unfortunately not available. The temperature differences between Cape Town on the one hand and Hermanus and Danger Point on the other will be considered in the discussion. For the present it is sufficient to call attention to the lower sea temperatures at Cape Town.

The tides are of the semidiurnal type, and the ranges are narrow as elsewhere along the Union coast, the mean high water of spring tides being 5 to 5½ feet above mean low-water springs. Low-water spring tides is between about 8 and 9 o'clock both mornings and evenings, and thus the algae growing at the lowest inter-tidal levels are subjected neither to the heat of the midday hours nor to the lowest nocturnal temperatures.

Terminology.

As compared with the previous paper, the algal vegetation has been dealt with to a greater extent in terms of associations and consociations. It has been easier to accomplish this with the west coast studies as a background, and this approach has been found more satisfactory in dealing with a small number of localities on a limited extent of coast-line. Description in terms of recognised vegetation units has an advantage in relation to horizontal as contrasted with vertical changes in vegetation. Observations are included on the inter-tidal levels and sequence of algal communities, but no attempt has been made to correlate the plant communities with the zones recognised by Stephenson for the south and west coast regions. This may be dealt with later in a more general paper.

Since marine algologists show greater divergence and less exactitude in their use of terms describing vegetation units than students of land vegetation, definitions are given below of the sense in which the terms are used in this paper.

Association and Terms used in Describing Associations.—By association is meant an assemblage of one or more species with one or more dominants, occurring under a characteristic range of conditions of sea temperature, substratum, salinity, exposure, and emersion. The term "emersion" is used for the condition of being uncovered by sea water. This is usually referred to in the literature as "exposure". Unfortunately "exposure" is also used for the degree of roughness of the sea to which the algae are subjected, and in this paper it is used in the latter sense only. While sea temperature, exposure, and substratum are simple environmental factors, emersion represents a period of time during which a plant or community is exposed to a complex of factors, some of them resulting from conditions of land climate, some from such topographical features as slope of rock or amount of shade, and some from the degree of exposure to spray and splash from the sea. Salinity variations also tend to represent a complex of

factors, since the presence of fresh water implies not only reduced salinity but also increased moisture, and frequently situations with a greater or lesser degree of protection from the full force of the sea. Determinations were made of the chloride content of a few samples of water by means of the silver nitrate titrimetric method and salinity estimated using Knudsen's formula ($S^{o}/_{oo} = 0{\cdot}03 + 1{\cdot}8050$ Cl. $^{o}/_{o}$).

It should be noted that although sea temperature is in itself a simple factor, the warmer waters of the Agulhas current have a higher salinity and probably lower nitrate and phosphate contents than west coast waters. Oxygen content decreases with a rise in temperature.

Further investigations are needed both for a fuller description of the associations and for a more exact account of the range of environmental conditions under which they occur. Such information may lead to changes in the units recognised as well as in their status.

In referring to the degree of density of algal growth, the term absolute frequency suggested by Arrhenius (1922) has been used. The term refers to the actual number of individuals per unit area covered by an association, and thus expresses the closeness of the association. The term is used here to denote the order of density, such as "high" or "low" absolute frequency.

Consociation.—This term is used in its usual sense of a community dominated by one of the dominant species of the association to which it belongs. This definition presupposes the association to have at least two dominants.

"Zonation" and "Zones".—These words are used in relation to the relative vertical sequence of algal communities, and thus refer essentially to the vertical distribution of algae in relation to tidal levels. The precise inter-tidal levels at which seaweeds grow can only be determined by exact measurements such as were made by Coleman (1933) and Zaneveld (1937), or more approximately they can be determined by frequent observations in localities where times of high and low water of spring and neap tides are available from published tide-tables as was done for the west coast.

It was only possible to make a limited number of observations of the relation of tidal levels to the vertical levels of algal species and communities in the localities under consideration, and thus the chief stress is laid on the inter-tidal sequence of algal zones with only general indications of their inter-tidal levels. Zonal sequence is referred to in relation to Low-Water Springs (L.W.S.), Low-Water Neaps (L.W.N.), High-Water Neaps (H.W.N.), and High-Water Springs (H.W.S.). These terms indicate the order of the mean level of the sea in each case. The phrase "mid-zonal level" indicates approximately half-way between L.W.S. and H.W.N.

Littoral and Sub-Littoral.—Littoral refers to that part of the shore between H.W.S. and L.W.S. In the previous paper the term was used for

that area of the shore from the upper limit of algal vegetation to the lowest level of L.W.S. On fuller reflection it seemed more satisfactory to confine the use of the term to tidal levels. For the most part the upper limit of the algal vegetation is about H.W.N.

The term sub-littoral is used for the area extending seawards from L.W.S. whether the *Ecklonia*-consociation extends to a somewhat higher vertical level or not. Consequently this term also is used entirely in relation to tidal levels, whilst in the previous paper small outliers of kelp left emergent at L.W.S. were regarded as belonging to the sub-littoral.

List of Species.

Chlorophyceae:

Cladophora capensis (Ag.) Kütz. (*C. Ecklonii*).

Codium fragile (Suringar) Hariot.

C. Stephensiae Dickinson (Dickinson, 1932).

Enteromorpha bulbosa (Suhr) Kütz. The material collected at Gansbaai corresponds closely with material in the Bolus Herbarium named *E. bulbosa* f. *africana* by Dr. G. F. Papenfuss.

E. compressa (L.) Grev.

Ulva Lactuca L.

U. uncialis. The material named *U. uncialis* in this paper corresponds to the material thus named in the Tyson collection at the Bolus Herbarium. Levring (1938) maintains that the South African material named *U. uncialis* corresponds to *U. rigida* J. G. Agardh. The material examined by Levring was obtained from Durban and Port Elizabeth. Papenfuss (1940 *b*) points out that *U. capensis* Aresch. has been regarded by some as synonymous with *U. rigida* and by others as relating to *U. uncialis.* He claims, however, that *U. capensis* and *U. rigida* are distinct, but states that whether *U. capensis* and *U. uncialis* are distinct can only be settled after studying Kützing's type of *U. uncialis*, which he has not been able to do. Suhr used *U. uncialis* as a manuscript name for material collected from the east coast of South Africa. Kützing's type was collected in Table Bay.

In view of the uncertainty indicated above, it seems best to use the name *U. uncialis* Kütz for the present.

Phaeophyceae:

Bifurcaria brassicaeformis (Kütz) Barton.

Bifurcariopsis capensis (Aresch.) Papenfuss (1940 *a*). (*Bifurcaria laevigata* Barton or *Pycnophycus laevigatus* Kütz.)

Chordariopsis capensis (Ag.) Kylin. (*Chordaria capensis* Aresch. or *C. flagelliformis* var. *capensis* Kütz.)

Colpomenia sinuosa (Roth) Derb. et Sol.

Dictyota dichotoma (Huds.) Lamour var. *intricata* (Ag.). (*Dictyota dichotoma* var. *implexa*.)

Ecklonia maxima (Osbeck) Papenfuss. (*E. buccinalis*.)

Iyengaria stellata Börgs. (Börgesen, 1939). This is regarded by Börgesen as identical with *Colpomenia capensis* Levring (Levring, 1938).

Sargassum heterophyllum (Turn.) Ag. The material collected corresponds to material (SS 14) so named in Stephenson's collection. Stephenson (1944) makes the following comment: "Under this name are here included both *S. heterophyllum* (Turn.) Ag. and *S. incisifolium* (Turn.) Ag., which have been shown by Papenfuss to be forms of the same species" (p. 349). The naming of this species is to be regarded as tentative.

S. longifolium (Turn.) C. Ag.

Splachnidium rugosum (L.) Grev.

Rhodophyceae:

Aeodes orbitosa (Suhr.) Schm.

Arthrocardia Stephensonii Manza (1937, 1940).

Carpoblepharis flaccida (Turn.) Kütz.

Caulacanthus ustulatus (Mert.) Kütz. *C. divaricatus* (Suhr.) Papenfuss resembles both *C. ustulatus* and *C. spinellus* in habit, and Papenfuss remarks that further study may show these plants to be co-specific but that it seems best to deal with them as separate species for the present. The South African plants are possibly all *C. divaricatus* (Suhr.) Papenfuss, but for convenience the name *C. ustulatus* (Mert.) Kütz is being used until a more critical study has been made.

Chaetangium ornatum (L.) Kütz.

Champia compressa Harv.

C. lumbricalis (L.) Desr.

Chondria capensis (Harv.) Falkenb.

Dicurella fragilis (Ag.) J. Ag.

D. scutellata (Her.) Papenfuss. (*D. flabellata* (J. Ag.) Harv.)

Gelidium cartilagineum (L.) Gaillon.

G. pristoides (Turn.) Kütz.

Gigartina radula Ag. It is recognised that the assemblage named *G. radula* may prove on further study to be either one variable species or to consist of more than one species (Isaac, 1937 *b*; Stephenson, 1944). Until taxonomic studies are conducted, however, the name *G. radula* is retained.

G. stiriata (Turn.) Aresch. Following the suggestion of Delf and Michell (1922), this species is regarded as including the less common tetrasporic plant named *G. Burmanni* J. Ag.

Grateloupia filicina (Wulf) C. Ag.

Gymnogongrus vermicularis (Ag.) J. Agardh.

Hildenbrandtia pachythallos Dickinson. Corresponds to SS 34 in Stephenson's collection.

Hypnea spicifera (Suhr.) Harvey.

Iridophycus capense (J. Ag.) Setchell and Gardner (Setchell and Gardner, 1936, 1937).

Pachymenia carnosa J. Ag.

Plocamium corallorhiza (Turn.) Harv.

P. cornutum (Turn.) Harv.

Porphyra capensis Kütz.

Pterosiphonia cloiophylla (Ag.) Falkenberg. This species is very closely related to *P. complanata* Schmitz, but in view of the different geographical distribution Papenfuss considers it best to retain the two species until fuller investigations are made (Papenfuss, 1943).

Suhria vittata (L.) J. Ag.

Tayloriella virgata (Ag.) Papenfuss. (*Polysiphonia virgata.*)

Wrangelia purpurifera (Harr.) J. Ag. Material identified by Dr. M. A. Pocock.

The Algal Vegetation of Gansbaai.

Observations were made from Stanford Cove to a little distance south of the Ocean Products Factory (fig. 3).

Topography of the Coast.

The coast is rocky, mostly quartzite of the Table Mountain series, with occasional small sandy beaches. Along most of the coast-line represented in fig. 3 the strike of the strata is more or less parallel to the sea. This is especially so from a little northwards of the swimming baths to the vicinity of the harbour. In places the strike of the strata is at an angle to the coast-line, especially between Stanford Cove and a little northwards of the Baths, and in the vicinity of the harbour and factory. The angle of the strike varies, but it is sometimes more or less at right angles to the coast-line. Where the strike is at an angle to the coast-line there may be promontories of greater or lesser length, and also narrow, steep-sided coves which frequently have miniature sandy beaches. The strata sometimes dip towards the sea, are sometimes upright, but the dip is mostly away from the sea, presenting a series of ridges between which are depressions. These depressions contain pools of greater or lesser depth and of varying size; there are also more or less permanent streams of sea water which may incorporate pools with a constant inflow and outflow during low tide.

Narrow elongated ridges of rock occur just beyond low-water mark, and these are thus permanent small islands. Another coastal feature, indicated in fig. 4, is a low, gently sloping platform (usually narrow) at about L.W.S.

FIG. 3.—Diagram of the coast-line from Stanford Cove to Gansbaai based on an aerial photograph taken in 1939. Scale, about 1/25,000.

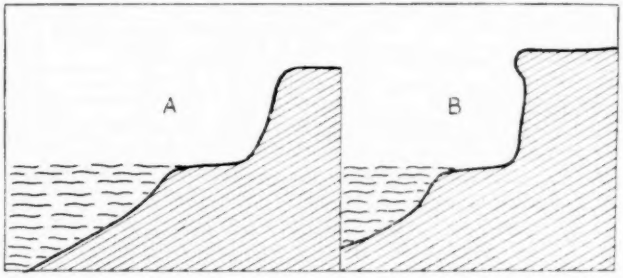

FIG. 4.

level, with a steep rise at its landward side and sometimes a fairly steep drop on its seaward side (fig. 4 A). The cliff rising steeply above the level of the sea may show an overhang (fig. 4 B).

Fresh water, sometimes fouled, runs into the sea at a number of places.

This is very noticeably the case just northwards from the harbour, where the rocks are backed by marshy ground, and again at the Swimming Baths. The general layout of the Baths is indicated in fig. 5. Fresh water flows from pipe A into the smaller bath B, which is at a somewhat higher level than the bath C, which is open to the sea at its lower end. Water overflows from B into C, G, and especially into the depressed areas D, which lie between B and the sea-wall E. Water collects in D, forming pools with waters of reduced salinity. The effect of reduced salinity is obvious on the

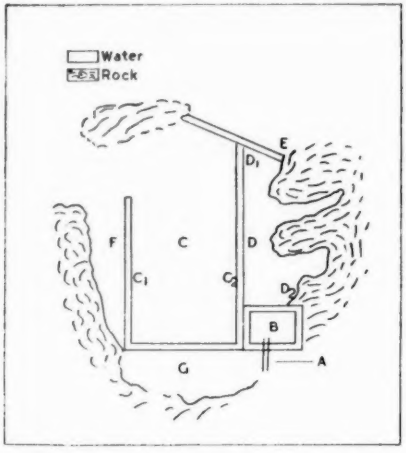

FIG. 5.—Diagrammatic representation of chief features of the Swimming Baths at Gansbaai.

seaweed vegetation in the vicinity of the Swimming Baths. The salinity determinations given below indicate the effect of the outflow of fresh water from A on the salinity of sea water in the vicinity of the Baths. The water samples were collected around 11 o'clock on 25th August 1946 (low water at about 8.30 a.m.):

Location of Sample.	$S^0/_{00}$.
C	31·36
D_1	9·14
D_2	3·88
F	34·5

It is clear from the above remarks that the shore presents a considerable variety of environmental conditions. Where the strike of the rocks is more or less parallel to the coast-line, their seaward edges frequently present situations directly exposed to the waves. In small bays behind jutting

rocks, and again along the sides of long, narrow, high-walled coves which occur where the strike of the strata is at an angle to the sea, there is much surf and swell but without the direct pounding action of the waves. Cliffs with or without an overhang, rising abruptly from narrow platforms, present situations where spray is constantly carried to heights above the level of H.W.S. (fig. 4). Lastly, there are very sheltered situations. All these environmental conditions have their effects on the algal vegetation. Still further modifications occur in sheltered situations where fresh water is present.

Zonal Sequence of Algae.

Only those features of the sub-littoral vegetation are noted which can be observed at L.W.S. or, at any time, at the surface of the sea. Within these limitations the most obvious feature is the prominence of *Ecklonia maxima*. The presence of *Sargassum longifolium* is also characteristic. It is thus convenient to characterise the sub-littoral vegetation as the *Ecklonia* consociation or *Ecklonetum*. This vegetation may extend upwards into the lower levels of the littoral.

The *Ecklonia* consociation may be succeeded vertically by

(*a*) The *Bifurcaria* association, dominated by *B. brassicaeformis*;

(*b*) The *Gigartina* association, characterised by *G. radula* and *G. stiriata*; or

(*c*) A mixed algal vegetation.

Where the lowest littoral level is occupied by the mixed algal vegetation, it may be succeeded vertically by the *Bifurcaria* association or, in places, by the *Gigartina* association.

The *Aeodes* association, which is dominated by *A. orbitosa*, occurs typically at a higher inter-tidal level than the preceding. It is succeeded successively by the *Gelidium* and *Porphyra* associations, the dominant species of which are *G. pristoides* and *P. capensis* respectively.

In places there is a noticeable interval of bare rock between the *Gelidium* and *Porphyra* associations. This zone is devoid, or nearly devoid, of algal growth, and corresponds to the Bare zone described for the west coast.

It should be noted that while on parts of the west coast *Chaetangium ornatum* forms a belt below the level of *Porphyra capensis*, the former species is neither sufficiently widespread nor of sufficient local abundance in the Gansbaai district to be regarded as forming a characteristic zonal community.

The fundamental zonal sequence of algae at Gansbaai is indicated in fig. 6.

While the zonal sequence is clear on fairly steep slopes and on vertical faces, it is less obvious on more gently sloping or irregularly shaped rock

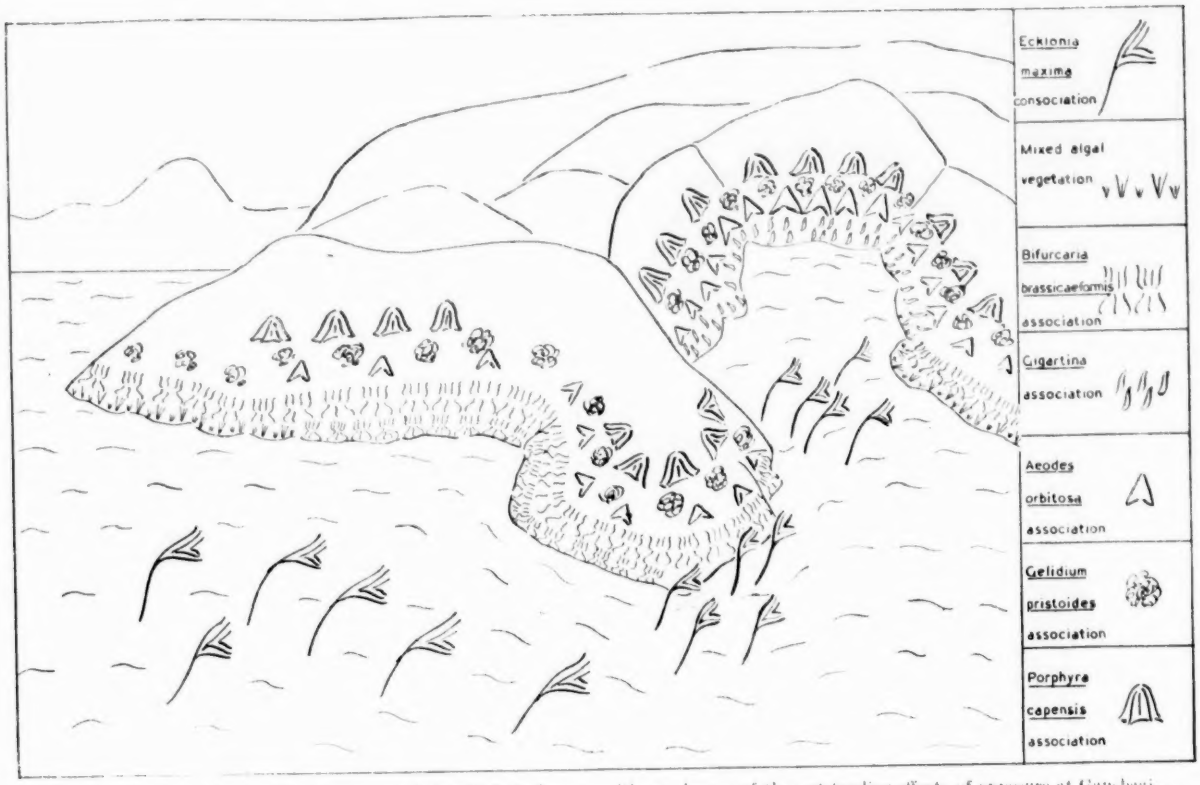

FIG. 6.—Diagram showing zonal sequence of the chief algal communities and some of the outstanding effects of exposure at Gansbaai.

masses, and sometimes it can only be recognised by careful observation. On more or less flat surfaces in sheltered or fairly sheltered situations, a vegetation consisting of a mixture of species occurs, including species not found in exposed situations. Such a vegetation is found on the more or less flat rocks below the factory and includes the following species: *Aeodes orbitosa*, *Bifurcaria brassicaeformis*, *Iridophycus capense*, *Gelidium pristoides*, *Splachnidium rugosum*, *Ulva uncialis*, *Cladophora*, *Gigartina radula*, *G. stiriata*, and jointed (Corallineae) and encrusting (Melobesieae) Corallinaceae. Prominent among the Corallineae is *Arthrocardia Stephensonii*, which forms small, dense hemispherical cushions in which only the apical parts of the individual plants are exposed. This mixed community passes below into the *Bifurcaria* association, and above into the *Aeodes* and *Gelidium* associations.

An overlapping of zonal communities at their upper and lower limits is of more frequent occurrence than such mixed algal communities. Thus in moderately sheltered situations the lower vertical limits of the *Bifurcaria* association may be invaded by *Gigartina radula*, while its upper limits may be invaded by *Aeodes orbitosa*. *G. radula* may also occur as an undergrowth to *A. orbitosa*.

The Chief Algal Communities.

Ecklonia *Consociation.*—This community is a consociation of the Kelp association described in the first paper of this series. *Ecklonia maxima* is the dominant species in the upper stratum visible at the surface of the sea. *Sargassum longifolium* is a characteristic species which can be observed close inshore. Plants of this species are large and luxuriant in their growth, and sometimes they form small or moderately extensive stands. It tends, however, to occur as an undergrowth to *Ecklonia*. How common *S. longifolium* may be further out to sea it was not possible to ascertain. In shallower water *Bifurcariopsis capensis* frequently occurs in the upper reaches of the sub-littoral. Two examples were observed of a fairly dense, local growth of this plant (society) on flat surfaces in shallow water a little out to sea. It is a very common species in the Gansbaai district, occurring in the upper sub-littoral and in rock pools from L.W.S. to mid-zonal level, but especially in rock pools at the lowest littoral levels. It was only very rarely found completely uncovered at L.W.S. *Pachymenia carnosa* deserves mention since, although not common, it occurs fairly constantly at wide intervals in the upper limits of the consociation, and because its relatively bright red colour stands out in contrast to the brown and yellowish-brown colours of the other seaweeds.

Suhria vittata, *Carpoblepharis flaccida*, and *Tayloriella virgata* were found as epiphytes on *Ecklonia maxima*. Where observation was possible,

Fig. 6.—Diagram showing zonal sequence of the chief algal communities and some of the outstanding effects of exposure at Gansbaai.

the sub-littoral was seen to have a dense undergrowth of encrusting Corallinaceae and in places a variety of Corallineae. The *Ecklonia* consociation is typically sub-littoral, only the upper parts of the thallus of the dominant species being emergent above the surface of the water. These parts are constantly wet, since they are tumbled about by the sea. Where the shore is gently shelving, the *Ecklonia* consociation may sometimes invade the lower littoral levels, forming a belt several feet across at L.W.S. Examples of this were observed in places towards Danger Point, to a lesser extent between Gansbaai and Stanford Cove, but especially below the factory at Gansbaai.

This consociation is a characteristic feature of the coast to the extremity of Danger Point Peninsula, there being only insignificant gaps in its continuous occurrence. It is also prominent off the eastern coast of Danger Point Peninsula.

Mixed Algal Vegetation.—This designation is a tentative one, since fuller investigation is required to describe it in detail and to resolve it into its constituent communities. As used in this paper, the term denotes the algal growth at the lowest littoral levels, where it does not consist of the *Ecklonia* consociation, the *Bifurcaria* association, or the *Gigartina* association.

At Gansbaai the mixed algal vegetation is on the whole poorly developed, in that at many points it is absent or represented by isolated clumps of seaweeds. As it is variable in composition it is difficult to describe.

The following are the commonest species:—

Champia lumbricalis.
Chondria capensis.
Gelidium cartilagineum.
Pterosiphonia cloiophylla.
Gigartina radula.
G. stiriata (this includes *G. Burmanni*).
Codium Stephensiae.
Encrusting corallinaceae.
Wrangelia purpurifera was common in January between the harbour and the Swimming Baths.

Corallineae are locally common, and include species of *Arthrocardia* (*A. Stephensonii*) and *Amphiroa*. *Hypnea spicifera*, *Plocamium cornutum*, and *Champia compressa* were also observed.

Champia lumbricalis, *Gelidium cartilagineum*, and *Plocamium cornutum* were found in more exposed situations. *Chondria capensis* occurs mostly in situations subject to swell and surf but with less direct wave action.

Codium Stephensiae occurs typically in sheltered situations on vertical rock faces, and it seems to be favoured by the proximity of brackish water.

The occurrence of *C. fragile* may also be noted. This is much less common in the localities studied, but in places on the south-eastern coast of Danger Point it was observed to be locally common.

Gigartina radula, *G. stiriata*, and species of Corallineae also occur in sheltered situations.

The occurrence of *Dictyota dichotoma* var. *intricata* as a rare species may be noted.

Gigartina *Association*.—The dominant species are *Gigartina radula* and *G. stiriata*, the latter including the less common *G. Burmanni*.

In dealing with the seaweed vegetation of the west coast, *Gigartina radula* and *G. stiriata* were treated as prominent species of the *Champia* association in less exposed places. Between Rooi Els and Gansbaai, however, *Champia lumbricalis*, although widely distributed, is not a prominent feature of the vegetation and at best is common only very locally; in sheltered places, on the other hand, *Gigartina* is very prominent and frequently forms communities of high absolute frequency. Thus it becomes expedient to delimit a *Gigartina* association. Two consociations can be distinguished, one dominated by each of the two species. In very sheltered situations, and especially on flat or gently sloping rock surfaces, *G. radula* dominates. In situations exposed to considerable swell and frequently to much surf, *Gigartina stiriata* dominates, provided there is no direct exposure to heavy wave action. Thus it frequently flourishes on the vertical walls of narrow gullies, usually where the strike of the rock is at an angle to the sea. Both species, but especially *G. radula*, are tolerant of brackish water, although it is not clear to what extent this is related to the coincidence of brackish water and sheltered situations.

This association usually occurs at a somewhat higher level than the mixed algal vegetation, and tends in sheltered situations to occupy the level characteristic of the *Bifurcaria* association of more turbulent waters. In places, however, the *G. radula* consociation may spread downwards to the lowest littoral levels.

Bifurcaria *Association*.—This association consists predominantly of *Bifurcaria brassicaeformis*, since the creeping rhizoidal habit of the lower parts of the thallus allows it to colonise appropriate habitats with considerable success and to the exclusion of other species.

This association is prominent and well developed at Gansbaai, and except for very sheltered situations is almost everywhere present. Although more characteristic of situations exposed to direct wave action, it is also found to some extent in more sheltered situations.

Bifurcariopsis capensis may be found among the plants of *Bifurcaria*. Although these plants may grow alongside each other they do not occupy the same vertical level, since *Bifurcariopsis* grows in depressions of the

rocky surface. Water accumulates in these depressions, and so the plants remain submerged to a greater or lesser extent.

The *Bifurcaria* association at Gansbaai frequently occurs directly above the *Ecklonia* consociation and thus often at the lowest littoral levels (Pl. IX), or between the two algal communities there may be a narrow interval of rock devoid of macrophytic algae, if we exclude encrusting Corallinaceae. The upper and lower limits of this association may be invaded by other algal species. This is especially the case on more or less flat or slightly sloping rock surfaces. As already mentioned, where it directly succeeds the *Ecklonia* consociation, isolated clumps of species characteristic of the mixed algal community may occur at its lower vertical limits.

A characteristic situation for this species is on isolated rocks a little out to sea, where it is constantly subjected to wave action together with much surf.

Aeodes *Association.*—This community is dominated by *Aeodes orbitosa* with which *Iridophycus capense* is associated to a greater or lesser degree. At Gansbaai *Iridophycus* is much less abundant, and extends upwards to a higher vertical level. The two species are somewhat similar in general appearance. *Aeodes orbitosa* in general attains larger dimensions than *Iridophycus capense*, from which it also differs in being more slippery and tougher to the touch and is usually less elongated. They are chiefly distinguished by the character of the holdfast and the presence or absence of a short stipe. The frond of *Aeodes* lacks a stipe, arising directly from a broad holdfast, while that of *Iridophycus* has a distinct although short stipe, an "apophysis" or transition region, and a slighter holdfast. The two species show decided anatomical differences.

Splachnidium rugosum and *Caulacanthus ustulatus* are occasional species, and are most typically found at the lower vertical limits. *Splachnidium* occurs less typically in the upper levels of the *Bifurcaria* association.

This is one of the three most prominent algal communities at Gansbaai, but it is not so prominent and well developed as the *Ecklonetum* and the *Bifurcaria* association. Although *Aeodes* can usually be distinguished as dominating a belt above that of *Bifurcaria brassicaeformis* or *Gigartina*, its vertical position relative to other species is less well marked than is the case with most of the other associations. This is due not only to a possible wider vertical range, but also to the fact that in general the absolute frequency of this community is less than, for example, that of *Bifurcaria brassicaeformis*.

It occurs throughout a considerable range of seashore conditions, but in situations exposed to rough seas it is either absent or sparse and the individual plants are much reduced in size. It flourishes in somewhat sheltered situations, in moderately exposed places, and in the neighbourhood of rapidly flowing sea water.

Gelidium *Association*.—This association, dominated by *Gelidium pristoides*, although widely occurring is not extensive, and except at its lower vertical limits it has a low absolute frequency. The lower plants are of a larger size than those at a higher inter-tidal level.

It is clear that this species can withstand quite heavy seas. The most flourishing individuals, however, were found growing on vertical rock faces in narrow gullies, where they are subject to swell and surf although not to direct wave impact.

Porphyra *Association*.—The *Porphyra* association is absent over much of the coast-line, but locally *Porphyra capensis* forms dense communities from which other macrophytic species are absent.

Of the macrophytic species, *Porphyra capensis* occupies the highest vertical level. Individuals may be found at lower tidal levels, but the *Porphyra* association is found only at higher inter-tidal levels.

The *Porphyra* association occurs in the Gansbaai district at two levels:

(1) From mid-zonal level to about H.W.N. This was the more normal situation.

(2) In places subjected to considerable upward splashing of spray it was observed above H.W.N., as on high vertical faces of cliffs, the bases of which are subjected to strong direct wave action. Such vertical faces often have a slight overhang (fig. 4, B).

Plants occurring at lower levels are of larger size and denser colour than those growing higher up, where dense communities of smaller pale, greenish-yellow plants were seen. Most of the spray-moistened *Porphyra* communities observed were outside the Gansbaai area and much nearer Danger Point.

At both vertical levels *Porphyra* avoids exposure to the direct impact of very strong wave action. Also it is somewhat tolerant of brackish water flourishing in the vicinity of freshwater streams running into the sea.

Rock Pool Vegetation.

There are numerous rock pools on this coast, especially along those parts where the strike of the strata is more or less parallel to the sea. They vary in size, depth, and inter-tidal level, and consequently they show considerable differences in seaweed vegetation. Only a few of the more outstanding features are noted here.

Bifurcariopsis capensis is the most common rock-pool species, and it constitutes the great bulk of pool vegetation near L.W.S. It is also found in pools at a higher vertical level along with *Bifurcaria brassicaeformis*,

which latter species becomes dominant at still higher levels. In these pools two zones can frequently be distinguished: an upper very narrow zone of *Chordariopsis capensis*, and a lower zone dominated by *Bifurcaria*. *Grateloupia filicina* may be common in still higher pools, where it is sometimes the only large species present. The highest pools are usually occupied exclusively by *Enteromorpha*, mostly *E. compressa*. In some of these pools both *Ulva Lactuca* and *Enteromorpha* occur: the *Ulva* in the deeper parts and *Enteromorpha* in shallower water. In the smaller pools at the same level

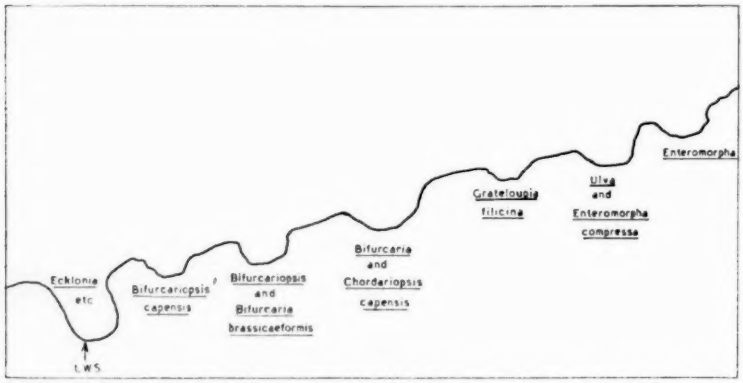

Fig. 7.—Vertical sequence of commonest rock-pool species at Gansbaai.

and in the highest pools, the vegetation consists entirely or chiefly of *Enteromorpha*. A few deep pools at L.W.S. contain *Sargassum longifolium*, *S. heterophyllum*, and *Ecklonia maxima*, as well as species characteristic of the mixed algal community. *Dicurella scutellata* and *D. fragilis* were also found in these pools. The vertical sequence of the commonest rock-pool species is shown in fig. 7.

Influence of Reduced Salinity.

Conditions of reduced salinity occur at a number of places along the coast, but chiefly a little northwards from the harbour, and at the Swimming Baths. The algal vegetation is strikingly affected by the proximity of fresh water, but these effects were not studied in detail, only the most outstanding features being noted. Where there is marked reduction in salinity and the substratum is permanently wet, submerged or partly submerged, a luxuriant vegetation of Chlorophyceae results. *Enteromorpha compressa* is the most common species, although *E. bulbosa* may be dominant

very locally. Other species found in such situations are *Ulva uncialis*,* *U. Lactuca*, *Cladophora capensis* and, locally, *Lyngbya*.

Where the reduction in salinity is not as great and there is no permanent wetness, *Porphyra capensis* was found to flourish. At the Swimming Baths, this species in addition to occurring at F (fig. 5) occurred also on the tops and sides of the walls (C_1 and C_2) of the Baths.

A number of species were found growing in the large Swimming Bath as well as at the outlet to the open sea. These species included *Grateloupia filicina*, *Gigartina radula*, *G. stiriata*, as well as *Ulva* and *Cladophora*.

The Algal Vegetation of Rooi Els.

Topography of the Coast.

The Rooi Els River at its lower end flows over a level stretch of sand. Further away from the sea its western bank is rocky, the opposite bank being sandy. Northwards from the small sandy beach the coast is rocky (Table Mountain Sandstone) and exposed (fig. 8). Shelving rock is practically absent, large boulders and vertical, or nearly vertical, rock faces characterising this area. Less exposed situations occur, in some of which the algae are subjected to considerable swell, in others to swell and surf, and in still others to relatively little water movement. Westwards from the river the coast is more varied, and comprises rocks, small sand beaches, and sandy beaches with scattered boulders. In September 1944 and October 1946 the dark brown waters of the Rooi Els ran into the sea, discolouring it extensively near the river's mouth. At a few places northwards of the Rooi Els River, trickles of fresh water ran over the rocks into the sea.

Algal Vegetation.

The littoral vegetation at Rooi Els agrees with that at Gansbaai in the luxuriant development of the *Bifurcaria* association, which forms a broad and dense belt above the level of the mixed algal vegetation, and also in the poor development of the *Gelidium* association, which has a low absolute frequency. The vegetation differs from that at Gansbaai in the poor development of *Aeodes orbitosa*, the individuals of which are small, not very common and very local. They are mostly found at the lower levels of the zone occupied by the *Gelidium* association. Another contrast with

* *Ulva uncialis* is a common and widely spread species. It occurs at all vertical levels, and although it is found growing under conditions of reduced salinity, it is not as closely associated with such situations as *Enteromorpha*. Observations indicate that it is not resistant to full emersion, since it is mostly, if not always, found where there is at least some water.

Gansbaai is the poor development of the *Ecklonia* consociation, which is very local in its distribution and, as far as could be ascertained, consisted only of small plants. *Sargassum longifolium* occurs but it would seem to be rare.

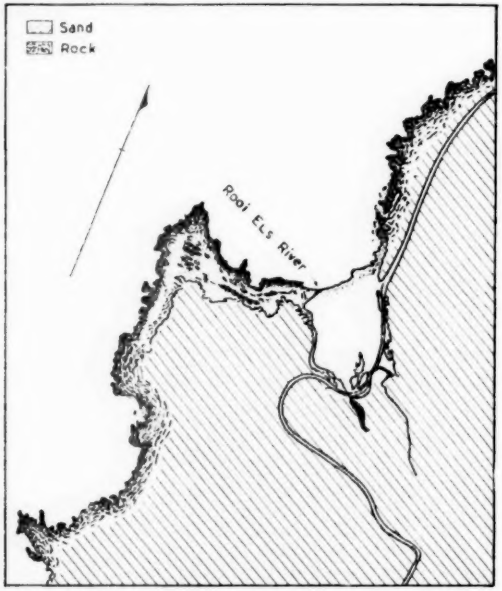

FIG. 8.—Diagram of coast-line in the region of Rooi Els River, based on an aerial photograph taken during a 1942–43 survey. Scale, about 1/18,000.

The zonal sequence is as follows:—

Sub-littoral.—Poor and local development of *Ecklonetum.*
Lowest Littoral.—Mixed algal vegetation. Well developed.
About L.W.N. to Mid-zonal Level.—
Bifurcaria association. Well developed.
Gelidium association. Poorly developed.
About H.W.N.—*Porphyra* association. Well developed.

In many exposed places there is little or no seaweed vegetation above the level of the *Bifurcaria* association.

The lowest littoral vegetation was much less closely examined than at Gansbaai. *Plocamium cornutum* and *Gelidium cartilagineum* are the most usual dominants. *Dicurella scutellata*, dark green *Hypnea spicifera*, *Sargassum heterophyllum*, and *Plocamium corallorhiza* are also characteristic plants at this level. *Hypnea* is usually local in its distribution, but it was

sometimes observed as a co-dominant with *Gelidium cartilagineum*. *Sargassum heterophyllum* is still more localised in its occurrence although in places it is common. *Plocamium corallorhiza* is nowhere very common but is widely distributed. Encrusting Corallinaceae occur as a sub-vegetation and sometimes show a luxuriant growth.

In situations exposed to direct wave action, and especially on vertical or nearly vertical rock faces, the lowest littoral level is occupied entirely, or almost entirely, by *Plocamium cornutum* and *Gelidium cartilagineum*. The former species occurs where the force of the sea is greatest, and in many places it occurs to the exclusion, or practical exclusion, of *Gelidium cartilagineum*. Where the sea is rough, *Bifurcaria brassicaeformis* is also a common species.

In situations sheltered from direct wave action, *Gigartina stiriata* and *G. radula* occur at lower littoral levels, although these species have a fairly wide vertical range.

Porphyra capensis is well developed in places subjected to much swell and spray—as on rock structures such as are illustrated in fig. 4. The incoming waves spend much of their fury in rushing over the lower horizontal rock platform and then surge up the steep rock face showering spray. In such situations *Porphyra* forms a broad belt which is frequently divisible into two sub-belts: a lower one of dark coloured plants, and an upper sub-belt of smaller, yellowish-coloured plants. *Porphyra* is also prominent on rocks in less exposed situations westwards of the river.

Rock Pools.—Bifurcariopsis capensis is a very common species, which in some pools is not only dominant but almost the only one present. *Chordariopsis capensis* is common. The following species are also found: *Dicurella scutellata*, *Sargassum heterophyllum*, *Dictyota dichotoma* var. *intricata*, and *Colpomenia sinuosa*. In some pools at the lower littoral levels a dense growth of jointed Corallinaceae was observed.

Influence of Fresh Water.

In September 1944 a dense algal growth consisting primarily of *Chaetangium ornatum* was observed on a low rocky ridge running across the mouth of the Rooi Els. These plants were regularly washed by water which was clearly of low salinity, as could be gauged from its brown colour due to the presence of the dark brown-coloured fresh water. In October 1946 the river was less swollen, and *Chaetangium ornatum* was not found where it had previously grown, although it was common on a rock-strewn sandy beach a little westwards. Young *Porphyra* plants were observed submerged in water near the river mouth in 1946, and two years earlier *Porphyra capensis* was found along with *Chaetangium ornatum* on the river bank a little

distance away from the sea. These *Porphyra* plants were smaller and paler than those subjected to water of higher salinity. A few small plants were found in a streamlet of running water which at the time had a salinity of 0·54‰. As would be expected, *Ulva uncialis*, *Enteromorpha compressa*, and *Grateloupia filicina* were found growing in water of reduced salinity, including water of 0·54‰.

The Algal Vegetation of Hermanus (including Onrustrivier).

Topography of the Coast.

The coast is rocky westwards of Hermanus and eastwards as far as Kwaaiwater. Beyond Kwaaiwater sandy beaches become a feature, and in the region of Mossel River they are predominant. The rock is Table Mountain Sandstone. We are concerned only with the rocky stretches. Seas are often very tumultuous, and in places the rocks arise in high vertical walls from the sea. This is especially the case at Kwaaiwater, as its name (Angry Water) implies. Thus, much of the coast is somewhat inaccessible, and more accessible parts are frequently somewhat barren. There are places, however, where a rich algal vegetation is found.

Seaweed Vegetation: General.

The general vertical sequence of algal communities above the level of the *Ecklonia* consociation is indicated below:

Mixed algal vegetation.
Bifurcaria association.
Gelidium association.
Porphyra association.

The absence of the *Acodes* association from this list will be noted. Its general absence and poor development is an outstanding difference between the Hermanus and Gansbaai districts. *Acodes orbitosa* is not absent although no very large plants were observed, but it is not sufficiently constant and abundant to form communities occurring at a more or less characteristic inter-tidal level. Neither is *Iridophycus capense* common.

A second contrast with Gansbaai is afforded by the much more restricted occurrence of the *Ecklonia* consociation. It is fairly well developed at Onrust. *Sargassum longifolium* is common in the upper sub-littoral along with *Ecklonia* (Pl. X), and very locally it may become dominant. *Bifurcariopsis capensis* also occurs in the upper sub-littoral.

Vegetation of the Lowest Littoral Level.

Four main types of vegetation were distinguished at the lowest littoral level:

(1) On high vertical or nearly vertical rocks subjected to very heavy seas *Plocamium cornutum* is the most characteristic species. Kwaaiwater affords the best example but the sheer vertical drop of the rocks and the wild seas make exact observation impossible.

In places where the sea is less violent, *Pterosiphonia cloiophylla* also occurs.

(2) In less exposed situations a number of species are found: the mixed algal vegetation; *Gelidium cartilagineum*, *Champia lumbricalis* and *Gigartina stiriata* are the most common. In addition to these three species and to those named under (1), the following occur:—

Chondria capensis.
Gymnogongrus vermicularis.
Champia compressa.
Pachymenia carnosa.
Hypnea spicifera and *Ulva uncialis.*

Of these, *Gymnogongrus* and *Ulva* seem to be very local in their occurrence. *Hypnea spicifera* may be locally common. *Pachymenia* and *Champia compressa* are occasional but they stand out rather prominently, *Pachymenia* on account of its size and relatively bright red colour, and *C. compressa*, although a small plant, on account of its occurrence in dense (although small) iridescent tufts.

(3) In fairly sheltered places the *Ecklonia* consociation invades the lower littoral levels, these plants being emergent to a greater or lesser extent, and many of them may be completely uncovered and unwetted for some time at L.W.S. To a lesser extent *Bifurcariopsis* and *Sargassum heterophyllum* may be emergent among plants of *Ecklonia*. The thallus of *Sargassum longifolium* may also be somewhat uncovered at the surface of the water (Pl. X).

(4) Lastly, the *Bifurcaria* association may occupy the lowest littoral levels, either with or without a narrow gap in the littoral zone between this association and the sub-littoral *Ecklonetum*. Isolated plants of the mixed algal community occur in places at the seaward limits of the *Bifurcaria* association.

Algal Vegetation above the Lowest Tidal Levels.

The *Bifurcaria* association is usually present both in exposed and in somewhat sheltered situations, even in the vicinity of fresh water flowing

into the sea. The association may be luxuriant or poorly developed, but in general it is not so prominent and well developed as at Gansbaai. The *Gelidium* association is well developed. Although the plants of largest size and most luxuriant growth occur at the lowest inter-tidal levels, the species occurs most characteristically at a level above the upper limits of *Bifurcaria brassicaeformis*. The association here often shows a high absolute frequency. The level occupied by the *Gelidium* association is relatively more prominent than at Gansbaai because of the poor development of *Aeodes* and *Iridophycus*, which together with *Splachnidium rugosum* may occur as occasional species of the *Gelidium* association. The *Porphyra* association is poorly developed. It is best developed in more sheltered situations, especially where fresh water runs into the sea.

Local Modifications of Seaweed Vegetation.

In sheltered places, which are not common, *Gigartina radula* is a feature at lower tidal levels, and the *Gigartina* association may in large measure occupy the level characteristic of the *Bifurcaria* association in less sheltered places, the latter association being absent. In a sheltered situation beyond Kwaaiwater, the *Gigartina* association is succeeded, on more or less flat rock, by a mixed vegetation of *Gelidium pristoides*, *Splachnidium rugosum*, *Gigartina* spp. (especially *G. radula*), *Chaetangium ornatum*, and *Iridophycus capense*. *Ulva uncialis* was found in pools and wet depressions among these plants.

Codium Stephensiae, growing on vertical rock faces and in shaded places, was only found in sheltered situations. It was observed at Onrust in the vicinity of fresh water.

Hildenbrandtia pachythallos was prominent at Onrust in the vicinity of fresh water. This species was also observed in other places in the region under consideration, but less abundantly.

In a few places the presence of fresh water had a marked effect on the seaweed vegetation. The most outstanding effects were a luxuriant development of the *Porphyra* association and, under conditions of still lower salinity, an abundant growth of *Enteromorpha compressa*, which was found flourishing in more or less fresh running water at about H.W.S. level in Bay View Hotel Bay.

Grateloupia filicina was also found in brackish water near Kwaaiwater. Worthy of note in Bay View Hotel Bay in early June (1946) was the abundant and almost continuous growth of jointed Corallinaceae in a large pool, the water of which was coloured brown at L.W.S. by an inflow of brown-coloured fresh water. A number of other species occurred in the neighbourhood of fresh water in this bay. Some of these were of unhealthy

appearance and others occurred in small numbers, so that there is uncertainty concerning the ecological significance of their occurrence. The presence of the following species, however, may be noted:—

Chaetangium ornatum, *Ulva uncialis*, *Gigartina radula*, *Bifurcariopsis capensis*, and *Bifurcaria brassicaeformis*.

Discussion.

Constant Features of the Seaweed Vegetation between Rooi Els and Gansbaai.

The significant (constant) features of the algal vegetation from Rooi Els to Gansbaai, as represented by the districts examined, are as follows:—

(1) An *Ecklonia* consociation dominated by *Ecklonia maxima*.

(2) The occurrence of *Sargassum*. *S. longifolium* is a common sub-littoral species in the Hermanus district and at Gansbaai but rare at Rooi Els, where, however, fewer observations were made. *S. heterophyllum* is an occasional or rare plant except at Rooi Els, where it was observed to be fairly common in places.

(3) A well-developed *Bifurcaria* association dominated by *B. brassicaeformis*.

(4) The *Gelidium* association dominated by *G. pristoides*.

(5) The presence in greater or lesser abundance of *Bifurcariopsis capensis*, *Splachnidium rugosum*, *Aeodes orbitosa*, *Iridophycus capense*, and *Porphyra capensis*.

The degree of development of these features varies. The *Ecklonia* consociation is prominent in the Gansbaai district but is not generally well developed either at Rooi Els or at Hermanus, although it is quite prominent at Onrust in the Hermanus district. The *Bifurcaria* association is consistently well developed. The *Gelidium* association shows its best development at Hermanus. The density and extent of the *Porphyra* association is very variable, but in general it is better developed at Rooi Els than at Hermanus. The greatest contrast is presented by *Aeodes orbitosa*, which is an outstanding feature at Gansbaai both in density of growth and size of individuals. It dominates a characteristic *Aeodes* association, while at Hermanus it is usually an occasional species.

The *Aeodes* association probably corresponds to the *Iridaea* association of the west coast. The similar species *Aeodes orbitosa* and *Iridophycus capense* were previously identified as *Iridaea capensis* on the basis of named material in the Tyson collection. This material was later studied and renamed by Dr. G. F. Papenfuss. The *Aeodes* association has subsequently been re-studied by the writer at Melkbosch, where the dominant species is undoubtedly *Aeodes orbitosa* although *Iridophycus capense* is present. This

is also the situation in the localities dealt with here, although on the south-eastern part of the Danger Point Peninsula, *Iridophycus capense* is dominant in a sandy bay strewn with outcrops of rocks.

Species of *Ulva* and *Enteromorpha* occur throughout the extent of coast-line under consideration. The South African species of these cosmopolitan genera occur locally over a wide extent of coast-line in the immediate vicinity of fresh water and where there is a permanently wet substratum for their growth. A vegetation dominated by them is thus best regarded as replacing locally a vegetation determined by the geographical factors operative within a region.

Vegetation of the Lowest Littoral Level.

The seaweed vegetation at the lowest littoral levels varies much from place to place. It may consist of the *Bifurcaria* association, of the mixed algal vegetation, or of an upward extension of the *Ecklonia* consociation. As already indicated the name "mixed algal vegetation" is tentative, and it should be possible after more extensive study to define a number of communities more precisely. The character of the vegetation at these lower inter-tidal levels is much affected by the degree of exposure to wave action, swell, and surf.

Factors Affecting Seaweed Vegetation.

The effects on seaweed vegetation of sea temperature, different degrees of exposure, and of salinity are considered below. The algal vegetation and sea-temperature conditions of the extent of coast-line dealt with in this paper are compared with those of the west coast—the subject of the first paper of this series. Comparison with the sea-temperature conditions and algal vegetation of warmer seas is reserved for future consideration.

Sea Temperature.—Mean annual temperatures and the mean maxima and minima of the mean monthly temperatures for Cape Town, Hermanus, and Danger Point are given in the Table on p. 153.

The data on which these values are based are meagre, and those for Cape Town are not for the same period as the data for Hermanus and Danger Point; also, it is not clear with what degree of care and accuracy the daily temperature observations were made. They give an indication, however, of temperature conditions in the localities under consideration.

Maximum temperature values are of considerable importance in relation to the distribution of seaweed species. According to Setchell (1920), at least the great majority of marine algae are normal to an amplitude of mean monthly maxima of not more than 5° C. As we have seen, the differences in the maxima of the monthly means between Cape Town on the one hand

TEMPERATURE VALUES AND DIFFERENCES FOR CAPE TOWN, HERMANUS, AND DANGER POINT.

	Cape Town (1934–1935).	Hermanus (1901–1903).	Danger Point (1901–1903).
Mean Annual Temperature, °C.	12·8	14·5	15·5
°C. higher than Cape Town	..	1·7	2·7
Mean of max. mean monthly temps., °C.	15·8	18·2	18·5
°C. higher than Cape Town	..	2·4	2·7
Mean of min. mean monthly temps., °C.	10·8	12·8	14·2
°C. higher than Cape Town	..	2·0	3·4

and Danger Point and Hermanus on the other are about half of this. There is direct and indirect evidence that while sea temperatures increase southwards along the west coast of the Peninsula (Gilchrist, 1902), they decrease northwards (Isaac, 1937 *a* and *b*) as far as the region between Hondeklip Bay and Luderitz or even further. Thus while common features can be expected for the west coast north of Cape Town and the region under consideration, decided differences might also be anticipated, while there are likely to be fewer differences between the west coast of the Peninsula and the coast between Rooi Els and Gansbaai. No temperature data are available for Rooi Els, but if the character of the seaweed vegetation is taken as a criterion, it is reasonable to assume that conditions are not very different from those at Hermanus and Gansbaai.

The most outstanding difference between Rooi Els to Gansbaai and the west coast north of the Cape Peninsula is the absence of the *Bifurcaria* and *Gelidium* associations from the latter. *Bifurcaria brassicaeformis* and *Gelidium pristoides* are probably absent north of Cape Town, and if present at all they must be rare. Between Rooi Els and Gansbaai the seaweed vegetation of the lowest littoral levels is more complex, varied, and comprises a greater number of common species. Outstanding in this connection is the less constant presence and lower absolute frequency of *Champia lumbricalis*, which is a very characteristic species of the colder west coast waters. *Porphyra capensis* is more abundant, and in general of larger size on the west coast north of Cape Town.

The contrast is less marked when comparison is confined to the west coast of the Cape Peninsula. The *Bifurcaria* and *Gelidium* associations occur in both regions, but while the *Bifurcaria* association is found along

the whole of the west coast of the Cape Peninsula, the *Gelidium* association occurs only along the southern half of this coast-line, from about Kommetje southwards. These two associations present a further contrast on the west coast, for while the *Bifurcaria* association is well developed, the *Gelidium* association is both rudimentary and local in its occurrence. The algal vegetation of the lowest littoral levels is more varied and complex on the west coast of the Peninsula, especially from Kommetje southwards, than it is north of Cape Town. In this respect it agrees more nearly with the region from Rooi Els to Gansbaai. The more constant presence of *Hypnea spicifera* in this latter region should be noted, although it does not show the same high absolute frequency which is a feature of Rheboksdam Bay at the southern end of the west coast.

The occurrence as rare plants in the localities under consideration, of species characteristic of still warmer waters, further emphasises the deviation of the seaweed flora and vegetation from that of the west coast. It must be emphasised, however, that citing rare species is a somewhat hazardous proceeding, since species common under certain environmental conditions and characteristic of those conditions are sometimes found very locally and usually as rare plants in most unexpected places. Still, attention may be called to the occurrence, for example, of *Dictyota dichotoma* var. *intricata* and *Iyengaria stellata*; comment has already been made on *Sargassum heterophyllum*. On the west coast, *Sargassum* occurs only in the Saldanha–Langebaan lagoon, in which conditions prevail that are not typical of the west coast.

The more frequent and abundant occurrence of *Gelidium cartilagineum*, a species more characteristic of the warmer waters of the south and south-eastern coasts, may also be noted.

The most outstanding general contrast between the west coast and the region under consideration is that *Laminaria pallida*, which is a constant feature of the west coast, is absent or rare east of Cape Point. Professor J. H. Day has collected it at Danger Point (personal communication), and I have seen specimens of the species thrown up on a sandy beach between Danger Point and Quoin Point. If it is present in the localities dealt with in this paper, it either occurs in sufficiently deep water so as not to be visible at the surface of the sea, is very local, or is rare. That this is a species essentially characteristic of the colder seas off the west coast is indicated by its increasing abundance with a fall in temperature in a northerly direction. A second contrast is the intermittent occurrence and low absolute frequency of *Champia lumbricalis* from Rooi Els to Gansbaai, and its much greater abundance and consistent occurrence along the entire west coast except for its low absolute frequency in such exceptional localities as Rheboksdam Bay and Saldanha.

Exposure.—The degree of exposure to wave action and the nature of the protection from the direct impact of the sea have an important effect on the character of marine vegetation.

The following conditions can be distinguished:—

(*a*) Exposure to full force of the sea. The species best able to withstand the direct battering of the waves are *Gelidium cartilagineum* and especially *Plocamium cornutum*. *Pterosiphonia cloiophylla* is also found in situations exposed to rough seas.

(*b*) Moderately exposed places. *Champia lumbricalis* and *Hypnea spicifera* are found in such places.

(*c*) Situations in which the plants, although not directly exposed to the beating of the waves, are exposed to considerable swell and surf, as in narrow channels with high, steep sides. *Chondria capensis* and *Gigartina stiriata* are characteristic species of such situations. Where *Ecklonia maxima* is found in the lower littoral levels it is often subject to considerable swell, and at this level it is absent where direct wave action is considerable.

(*d*) Moderately sheltered places. *Splachnidium rugosum* and *Iridophycus capense* occur. *Porphyra capensis* flourishes best in somewhat sheltered places. The occurrence of small pale plants at a high level on steep rocks above wild seas is not in essential contradiction to this statement, since in such places the plant is mostly wetted by spray and splashing and is not constantly subject to direct wave action. The occurrence of *Porphyra* above high-water level in exposed situations has been described for other geographical regions: for *P. leucostica* in the western Mediterranean (Feldmann, 1937) and for *P. umbilicalis* in the Færöese (Börgesen, 1905).

(*e*) Sheltered situations in which the plants are exposed to neither heavy wave action nor to much swell. This may occur on flat or gently sloping rock surfaces cut off somewhat from the sea by large rocks at a lower inter-tidal level or out at sea. *Gigartina radula* is the most characteristic species in such places. Jointed corallines and *Codium Stephensiae* also occur.

Different species show varying degrees of exclusiveness in regard to the environmental conditions under which they grow. Thus, while both *Gigartina stiriata* and especially *G. radula* are found in very sheltered places, the former also grows where it is subject to much swell, in which situations *G. radula* is either absent or rare. Although *G. stiriata* occurs in both habitats, it is more characteristic of places subjected to considerable swell. *Gelidium pristoides* may be found exposed to heavy seas, in sheltered places, or where it is subject to much swell. Lastly, it may be mentioned that *Aeodes orbitosa*

grows under a variety of exposure conditions, but it flourishes best in moderately exposed to somewhat sheltered places; where there is exposure to heavy seas it is either absent or of small size and low absolute frequency. Occasional individuals of a species may be found in quite unexpected places. Thus, although *Plocamium cornutum* is found typically where it is subjected to heavy seas, yet small clumps of this plant have been found in the most sheltered places.

Reduced Salinity.—Fresh water in streams and trickles runs into the sea, at least during certain periods of the year, at a number of places at Rooi Els, Hermanus, and Gansbaai. The presence of fresh water in the sea is often easily detected by the brown colour of the fresh water. At L.W.N. and L.W.S. an appreciable number of species were found growing either immersed in, or in the vicinity of, more or less fresh or brackish water. Some were found only infrequently in such situations, and before they can be listed as characteristically tolerant of reduced salinity, more extended observations are needed as to the length of time they can withstand the influence of water of reduced salinity and retain a healthy condition. There is the further complication that brackish water is usually found in more or less protected situations. In some cases this may be the master factor, although a degree of tolerance to reduced salinity is implied. Certain species, however, are found so constantly in situations of reduced salinity and show such flourishing growth that it is reasonable to assume that such conditions are favourable to them. This applies to the following species:—

Enteromorpha compressa.
E. bulbosa.
Ulva uncialis.
Codium Stephensiae.
Grateloupia filicina.
Chaetangium ornatum.

Of these the most constant are various forms of *Enteromorpha*, including *E. bulbosa* and especially *E. compressa*. Near the harbour at Gansbaai these species form extensive communities of high absolute frequency (mostly in rock pools of greater or lesser depth), where fresh water flows over the rocks to the sea. The pre-eminently euryhaline character of *E. compressa* is indicated by its frequent occurrence in rock pools at a high vertical level in the inter-tidal zone. Here at times it may be assumed that the species is subjected to salinities higher than that of the open sea, although no analyses were made. The occurrence of a dense vegetation of the species at salinities of 9·14‰ and 3·9‰ at times of observation has been recorded in this paper. *Ulva uncialis* and *Grateloupia filicina* were also observed under conditions of reduced salinity, but where the reduction is very marked

these species seem to be neither as abundant nor as constant as *Enteromorpha*, although both were found growing along with *Enteromorpha compressa* in a fast-flowing streamlet which at the time of observation had a salinity of only 0·54‰. *Grateloupia filicina* is known to favour the proximity of fresh water on British coasts (Newton, 1931), and may be found growing on rocks, where fresh water runs into the sea. Lyle remarks that on the coasts of Guernsey this species is found "Where the water is clear and flowing quickly" (1920, p. 30).

The presence of *Grateloupia filicina* in shallow rock pools at a high vertical level suggests that it is tolerant of increased salinity, being thus like *Enteromorpha* an euryhaline species. Plants of *Cladophora*, including *C. capensis*, also occur where there is an admixture of fresh water.

Codium Stephensiae and *Chaetangium ornatum* were typically found in the proximity of fresh water running into the sea. At L.W.S. the former species is usually completely emergent, and as the tide rises there will inevitably be a rapid influx of sea water into the neighbouring brackish water. Similar considerations frequently apply to *Chaetangium ornatum*, but this species was found growing submerged (de Kelders), or partly submerged (Rooi Els), in more or less fresh water during low tide.

Two further species call for comment: *Gigartina radula* and *Porphyra capensis*. The former is tolerant of some reduction in salinity but there is no evidence that it is favoured by reduced salinity. Plants of *Porphyra capensis* were seen washed by the waters of the Rooi Els River, and were found even in flowing water which had a salinity of 0·54‰. These latter, however, were less luxuriant in their growth than those in the same locality growing under conditions of normal salinity. On the other hand, it was observed many times that plants of *Porphyra capensis* frequently showed more luxuriant growth, and the *Porphyra association* a higher absolute frequency, in the vicinity of fresh water.

The protected character of these situations, however, may be important, since *Porphyra* is emergent for a considerable proportion of each tidal period when it would not be subjected to an admixture of fresh water except during heavy rain. If we take Zaneveld's calculations for a corresponding level on the coast of Holland (1937), it would seem that the upper limit of the *Porphyra* association is emergent for over 70 per cent. of the year. It is interesting to note that Feldmann (1937) describes *P. leucostica* in the western Mediterranean as an euryhaline species.

Summary.

1. The sea temperatures at Hermanus and Danger Point, 5 miles from Gansbaai, are higher than at Cape Town. The difference between the first

two localities is small. No data are available for Rooi Els, but if the character of the seaweed vegetation is taken as a criterion, the sea temperatures are of the same order throughout the region under consideration.

2. The vegetation is described as far as possible in terms of associations and consociations. Definitions are given of these terms as well as of the following: emersion, exposure, absolute frequency, zonation, littoral and sub-littoral.

3. A list of the species considered, with systematic notes where necessary, is included.

4. The algal vegetation at Gansbaai is described in detail, and general comments on the seaweed vegetation of Rooi Els and the Hermanus district (including Onrustrivier) are added, in which differences and similarities to the algal vegetation of Gansbaai are stressed.

5. The *Ecklonia* consociation, dominated by *E. maxima*, is a constant feature, although it is poorly developed at Rooi Els and Hermanus. It is usually sub-littoral, but in places it invades the lower littoral levels.

6. *Sargassum* occurs in the upper sub-littoral and the lower littoral. *S. longifolium* is common at Gansbaai and Hermanus, while *S. heterophyllum* is more prominent at Rooi Els.

7. The *Bifurcaria* association, dominated by *B. brassicaeformis*, the *Gelidium* association, dominated by *G. pristoides*, and the *Porphyra* association, dominated by *P. capensis*, occur in order of increasing vertical level in all the localities studied. Of these, the *Bifurcaria* association shows the most luxuriant development.

8. At Gansbaai the *Aeodes* association, dominated by *A. orbitosa*, is a prominent feature. It is absent or poorly developed at Hermanus and Rooi Els, although *A. orbitosa* and *Iridophycus capense* are constant species.

9. In places a "mixed algal vegetation" occurs at the lowest inter-tidal levels. It comprises several species, but sometimes one or two dominate. Thus in very exposed places the vegetation may consist almost entirely of *Plocamium cornutum*.

10. In sheltered situations the *Gigartina* association is characteristic of lower inter-tidal levels. It is dominated by *G. radula*, except where there is much swell, in which case *G. stiriata* is dominant. Swell also favours the growth of *Chondria capensis*.

11. *Codium Stephensiae* is characteristic of sheltered places, especially in the presence of fresh or brackish water. *Porphyra capensis* flourishes best in moderately sheltered places.

12. *Gelidium cartilagineum* and especially *Plocamium cornutum* are characteristic of the most exposed situations. *Pterosiphonia cloiophylla* may also occur in exposed places.

13. Reduced salinity results in an abundant growth of *Enteromorpha*.

Ulva, *Grateloupia filicina*, and *Chaetangium ornatum* are among the species characteristic of reduced salinity.

14. The occurrence of a number of other species in relation to exposure and reduced salinity is considered.

15. *Laminaria pallida* is absent (or rare) between Rooi Els and Danger Point, while it is a constant feature of the seas off the west coast. The intermittent occurrence and low absolute frequency of *Champia lumbricalis*, a constituent of the mixed algal vegetation, presents a contrast to its abundance and constant occurrence on the west coast.

16. The extent of coast-line under consideration presents a greater contrast to the west coast north of Cape Town, where both the *Bifurcaria* and *Gelidium* associations are absent, than to the west coast of the Cape Peninsula.

17. The *Bifurcaria* association occurs along the entire west coast of the Cape Peninsula, and the *Gelidium* association is sporadically present from Kommetje southwards. The similarity between the extent of coast-line under consideration and the west coast of the Peninsula is further marked by the greater complexity of the algal vegetation at the lowest tidal levels in both as compared with the coast north of Cape Town.

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Ecklonia maxima and, emergent at a higher vertical level, *Bifurcaria brassicaeformis*; L.W.S., Gansbaai.

Photo: Wm. Edwyn Isaac. *Neill & Co., Ltd.*

Part of upper sub-littoral showing a mixture of *Echinus miliaris* and *Strongylocentrotus lamprdiens*; L.W.S., Hermanus.

Photo: Wm. Edwin Isaac. *Neill & Co., Ltd.*

THE WARM SPRING ON BUFFELSHOEK, NEAR THABAZIMBI, TRANSVAAL.

By Leslie E. Kent and H. D. Russell.

(With four Text-figures.)

(*Communicated by permission of the Honourable the Minister of Mines.*)

(Read March 19, 1947.)

Abstract.

A hitherto undescribed thermal spring rises from Waterberg sandstone on the farm Buffelshoek, 12 miles east-north-east of the Thabazimbi iron ore mine. The water issues at a temperature of 30·6° C., the daily discharge being about 18,000 gallons. Chemical analyses gave a total mineral content of 623·9 mgm. per litre, the dominant ions being Na', Ca'', Cl', SO_4'', and HCO_3'. Several analyses have been added for comparison; one, not previously published, is of water from the hot spring at Warmbaths.

Nitrogen, together with argon and its congeners, form no less than 99·5 per cent. of the gas bubbling up through the water at Buffelshoek. Attention is drawn to spring gases with similar compositions at another locality in the Transvaal, and also in England, Switzerland, and Madagascar. A generally held opinion that carbon dioxide, hydrogen sulphide, and the lower hydrocarbons are the chief gases escaping from spring waters is criticised.

The geological evidence indicates that the Buffelshoek spring is meteoric in origin. The flow down the artesian slope is assumed to be mainly in Bushveld granite, and this assumption is in agreement with the composition of the water.

Introduction.

About midway between Thabazimbi and Rooiberg there is a small thermal spring that is virtually unknown, even to the inhabitants of these nearby mining camps. It lies on portion C of the farm Buffelshoek 1314, in the Waterberg district of the Transvaal, the latitude and longitude being 24° 34′ S. and 27° 36′ E.

By road Thabazimbi and Rooiberg are 18 and 19 miles away respectively. Public transport is provided by buses of the South African Railways' Road Motor Service between Warmbaths and Matlabas.

Description of the Spring.

The spring emerges at an altitude of approximately 3,490 feet on a tiny island in an intermittent stream known as the Sterk river. This island rises only 3 feet above the normal level of the stream and is therefore often submerged for a few hours when the river comes down in flood.

Excavation of the muddy alluvial sand showed that the warm water issues from a single orifice in coarse-grained Waterberg sandstone. A plume of coarse sand flutters over this eye but is broken up at irregular intervals by surges of gas. Although somewhat tortuous, the orifice is large enough and straight enough to enable the arm to be inserted as far as the elbow.

The spring is seldom used for bathing, and until 1944 the water was allowed to run into the western channel of the river; the flow has since been diverted into an irrigation furrow.

Measurements of Flow and Temperature.

The following measurements were made:—

	October 2, 1944.	*September* 21, 1946.
Flow in Imperial gallons per 24 hours .	17,000	19,000
Temperature in the orifice . .	30·6° C. (87° F.)	30·5° C. (86·9° F.)

On Meinzer's classification this is a discharge of 5th magnitude.

Gas is exuded at the rate of approximately 140 litres (5 cubic feet) per 24 hours.

Physical Properties of the Water.

The water is odourless and, when the pool is undisturbed, colourless and clear. It has a slightly brackish taste.

The specific resistance and pH value are given at the bottom of the Table on p. 163.

Chemical Analyses.

(a) *Water.*—The first sample was taken by Dr. T. Ockerse of the Department of Health on April 4, 1941, in the course of his extensive investigation of the fluorine content of South African natural waters; the other was collected by the writers on October 1, 1944. The results of the analyses are given in the Table on p. 163. For comparison there has been added a recent and unpublished analysis of water from the well-known Warmbaths spring, 48 miles east-south-east of Buffelshoek.

	Buffelshoek Thermal Spring.				Warmbaths Spring.	
Sample collected	4.4.41.		1.10.44.		14.9.40.	
Ions.	Mgm. per Litre.	N/1000.	Mgm. per Litre.	N/1000.	Mgm. per Litre.	N/1000.
NH_4'	n.d.		nil		n.d.	
Na'	149·3	6·49	151·6	6·59	132·5	5·76
K'	3·1	0·08	5·7	0·15	2·9	0·07
Li'	n.d.		nil		n.d.	
Mg''	3·1	0·26	4·7	0·39	1·8	0·15
Ca''	31·0	1·55	27·1	1·35	13·0	0·65
Fe''', Al'''	n.d.		nil		n.d.	
Sum of Cations	186·5	8·38	189·1	8·48	150·2	6·63
Cl'	134·9	3·80	138·5	3·91	85·2	2·40
Br', I'	n.d.		n.d.		n.d.	
F'	6·4	0·34	6·6	0·35	11·0	0·58
SO_4''	35·5	0·74	35·1	0·73	12·1	0·25
HCO_3'	213·5	3·50	213·5	3·50		
CO_3''	nil		nil		102·0*	3·40
NO_3'	nil		nil		nil	
Sum of Anions	390·3	8·38	393·7	8·49	210·3	6·63
Total sum of ions	576·8	16·76	582·8	16·97	360·5	13·26
SiO_2	n.d.		44·8		48·2†	
Totals			627·6		408·7	
Residue on evaporation at 95° C.	512·0		459·0		390·0	
Permanent hardness	nil		nil		nil	
Temporary hardness as $CaCO_3$	90·0		87·0		40·0	
Alkalinity as Na_2CO_3	90·1		93·3		137·8	
pH	7·6		7·1		8·65	
Specific resistance (ohm cm.) at 60° F.	1585		n.d.		1800	

Analyst: W. Sunkel, Division of Chemical Services, Pretoria.

* Total carbonate expressed as CO_3'', but HCO_3' must also be present.

† By Division of Chemical Services, Johannesburg, on a sample collected in March 1944.

The analyses were recalculated in terms of hypothetical salines.

	Buffelshoek Thermal Spring.				Warmbaths Spring.	
Date collected . .	4.4.41.		1.10.44.		14.9.40.	
Salines.	Mgm. per Litre.	N/1000.	Mgm. per Litre.	N/1000.	Mgm. per Litre.	N/1000.
NaF . . .	14·3	0·34	14·7	0·35	24·4	0·58
NaCl . . .	217·4	3·72	219·8	3·76	136·2	2·33
Na_2SO_4 . . .	52·6	0·74	51·8	0·73	17·8	0·25
$NaHCO_3$ . . .	141·8	1·69	147·0	1·75	nil	
Na_2CO_3 . . .	nil		nil		137·8	2·60
KCl . . .	6·0	0·08	11·2	0·15	5·2	0·07
$Ca(HCO_3)_2$ . .	125·6	1·55	109·3	1·35	nil	
$CaCO_3$ . . .	nil		nil		32·5	0·65
$Mg(HCO_3)_2$ . .	19·0	0·26	28·5	0·39	nil	
$MgCO_3$ . . .	nil		nil		6·3	0·15
Total sum of salines .	576·7	8·38	582·3	8·48	360·2	6·63
Excess HCO_3' . .	nil	nil	0·6	0·01	nil	nil
SiO_2 . . .	n.d.		44·8		48·2	
Totals . . .		8·38	627·7	8·49	408·4	6·63

From a study of recent chemical literature Roy (13) has concluded that at the concentrations characteristic of natural waters silica is in the ionic condition. Now in these analyses summation of the milli-normalities reveals in each case an almost exact balance between cations and anions. In these rather siliceous waters, therefore, the silica can hardly be present to any appreciable extent in the ionic condition (as anions such as SiO_3'' or $HSiO_3'$) or the ionic balance would be upset. The analyst is thus justified in returning it as SiO_2, which is perhaps preferable to H_2SiO_3, the stable existence of which in the free state has not been demonstrated. Most of the silica is probably present as composite particles, a small proportion of which may be of colloidal dimensions.

A further sample of water from the Buffelshoek spring was evaporated to dryness in a platinum basin and the residue submitted to Dr. B. Wasserstein of the Geological Survey for spectrographic examination. His results follow:—

Major constituents . .	Na, Ca, K, Mg, Si
Minor constituents . .	Li, Ba, Sr, Al, B
Trace elements . . .	Pb, Mn, Mo, Sn(?), Fe
Elements looked for and proved to be absent . . .	V, Cr, Co, Ni, Zn, Ga, As, Rb, Y, Ag, Cd, In, Sb, Cs, W, Hg, Tl, Bi

(b) *Gas.*—Samples of the gas issuing with the water were collected on several occasions. The composition was found to be:

	October 1, 1944.	December 1, 1944.
Oxygen	0·5	0·3
Carbon dioxide . . .	nil	nil
Methane	slight trace	trace
Hydrogen	nil	nil
Nitrogen + rare inert gases (by difference)	99·5	99·7
	100·0	100·0

Analyst: Fuel Research Institute of South Africa.

The analyses were carried out by the usual absorption methods, the residue being nitrogen and the rare atmospheric gases. Its density was found to be appreciably less than air, but unfortunately no apparatus was available for determining the relative proportions of nitrogen and rare gases.

Non-Combustible Gases from Thermal Springs.

Here attention may be drawn to an assertion made by Tolman (15) in his well-known work *Ground Water*. Writing of springs in general he states:—

"The spring depression may be in alluvial material or solid rock. In either case it is usually floored with dancing sand, and the pool is agitated by the ascending water currents or is bubbling with escaping gases, *chiefly carbon dioxide, hydrogen sulphide, and hydrocarbon gases* (bubbling springs)." (Italics are ours.)

No mention is made of air, yet in many springs, and especially those of meteoric origin, the gas is atmospheric air which is generally deficient in oxygen. An extreme case of deoxygenation occurs at Buffelshoek. Admittedly carbon dioxide and hydrocarbon gases (and hydrogen), either singly or in varying mixtures, make up the bulk of many spring gases; but at many "sulphur springs" the gas, although smelling strongly of hydrogen

sulphide, is found on careful analysis to contain only a very small amount of it.

Several analyses have been published of non-combustible gases from thermal springs in South Africa. They are arranged below in order of decreasing oxygen content. Analyses of gas from two well-known American thermal springs have been added for comparison.

	Dry air.	Letaba spring, Transvaal (6).	Zwartkops thermal aterian borehole, C.P. (11).	Loubad spring, Transvaal (7).	Pivaans river spring, Natal (12).	Thundering, Georgia, U.S.A. (5).	Warm, Georgia, U.S.A. (5).
Oxygen .	20·99	20·5	11·54	11	0·65	20·87	13·91
Nitrogen + argon, etc.	78·98	79·5	85·03	87	91·96	79·01	85·50
Carbon dioxide	0·03	trace	3·43	2	7·39	0·12	0·59
Methane .	nil	nil	..	nil	..	nil	nil
Hydrogen .	nil	nil	trace	nil	..	..	..
Totals .	100·00	100·0	100·00	100	100·00	100·00	100·00
Temp. of water .	..	40·6 C.	54·4° C.	33·0 C.	40·5° C.	23·3 C.	31·0 C.

Gas collected by Mr. H. D. le Roex in June 1939 at "Die Oog", a thermal spring rising from a fault on the farm Rietfontein 1042 in the Potgietersrust district, was found on analysis to contain no less than 98·8 per cent. of "nitrogen". Apart from these two South African examples a search of the literature disclosed several other cases of thermal spring gases composed almost entirely of nitrogen plus the rare atmospheric gases. Three of these are given in the Table on page 167.

Versveld (16) reported that the spring at Warmbad, South West Africa (temp. 38° C.), emits gas that is practically pure nitrogen; oxygen, hydrogen, and carbon dioxide are absent. Here it is interesting to note that an earlier observer (4), presumably without testing it, stated that the gas was carbon dioxide.

Geology.

The farm Buffelshoek 1314 (former number 799) falls within Geological Survey Sheet 10, Nylstroom, which was published in 1912; but the position of the thermal spring is not marked on the map and no mention of it is made in the Explanation (8). In 1941 the area was investigated by J. W. du Preez, who wrote (2): "Of general interest is a tepid spring at the contact

of a diabase *sill* and Waterberg sediments, occurring on Buffelshoek, near the homestead of Mr. Fouché. The water, apparently charged with *carbon dioxide*, emanates along the lower contact of the sill." (Italics are ours.) In 1944 the area was remapped by H. D. Russell on a fairly large scale—250 Cape roods to the inch (*i.e.* 1 : 37, 188).

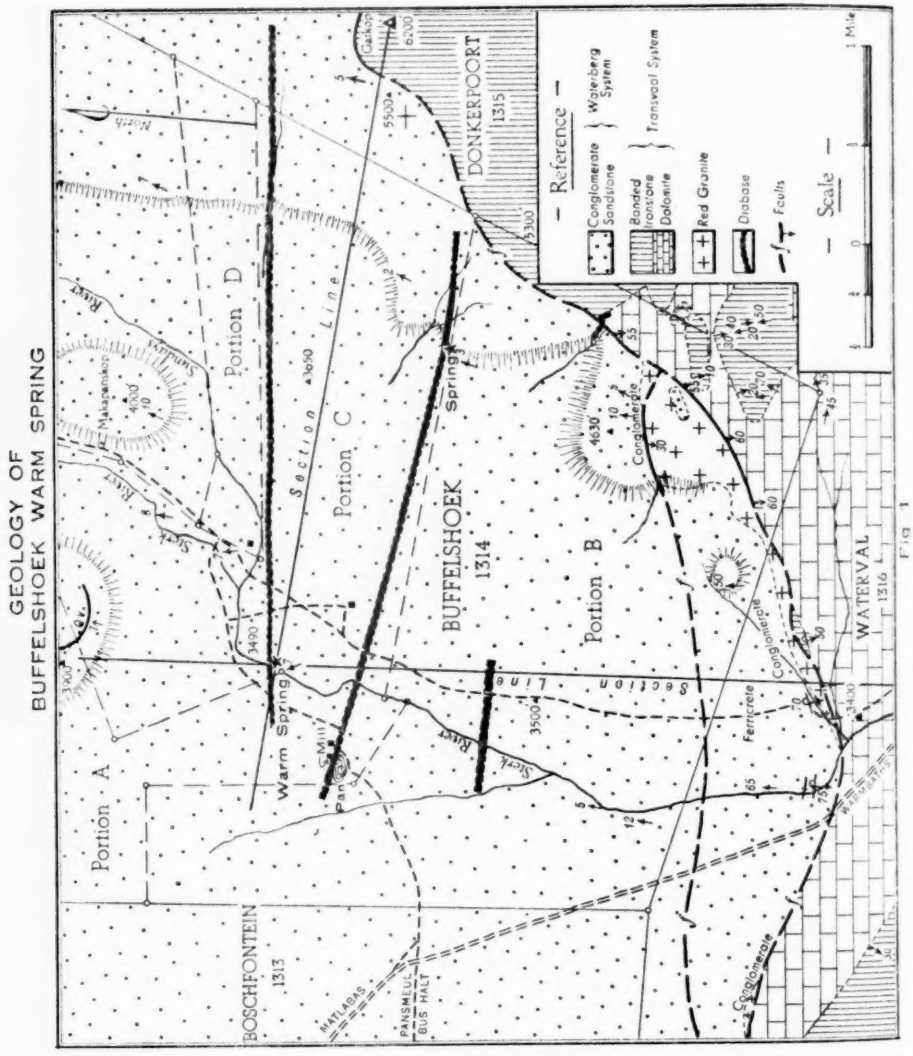
	Rietfontein 1042, Transvaal.	Buxton, England (14).	Horse spring, Leuker, Switzerland (3).	Ranomafana-s.-Namorona, Madagascar (9).
Oxygen	0·8	..	nil	trace
Nitrogen	98·8	99·12	97·4	97·55
Argon + krypton + xenon			1·6 (99·0)	1·35 (99·46)
Helium + neon				0·56
Carbon dioxide	..	0·88	0·9	0·55
Methane	0·4	..	..	slight trace
Totals	100·0	100·00	99·9	100·01
Temp. of water	39·5° C.	27·7° C.	46·0° C.	

Analyst Rietfontein gas: C. F. J. van der Walt,
Division of Chemical Services, Pretoria.

With the exception of the south-east corner, where Red granite, and dolomite and associated banded ironstones of the Transvaal system are found, the whole farm is underlain by sandstones and conglomerates of the Waterberg system. Northwards these latter give rise to the impressive escarpment of the Kransberg where the Sterk river and its large tributary the Sundays have their sources. Two isolated sandstone hills lie to the north and north-east of the spring. To the east the country is dominated by the twin peaks of Gatkop. This mountain, capped with banded ironstone, rises to over 6,000 feet above sea-level and provides the spring with a scenic background of rugged grandeur.

An idea of the topographic relief is given by spot heights (adjusted aneroid readings) on the map, fig. 1.

The sandstones and conglomerates are quite typical of the Waterberg system. The basal conglomerates, which are exposed resting on Red granite in the south-east corner of the farm, consist of boulders up to 3 feet in diameter of medium-grained Red granite set in an arkosic groundmass. The possibility exists that some of these conglomerates and associated pebbly sandstones are actually of pre-Waterberg age. From the hydro-


GEOLOGY OF
BUFFELSHOEK WARM SPRING
Portion A
Portion D
Portion C
Portion B
BUFFELSHOEK
1314
BOSCHFONTEIN
1313
DONKERPOORT
1315
WATERVAL
1316
Warm Spring
Section Line
Reference
Conglomerate
Sandstone
Waterberg System
Banded Ironstone
Dolomite
Transvaal System
Red Granite
Diabase
Faults
Scale
1 Mile
Fig 1

logical standpoint, however, there is no need to separate them. In the vicinity of the spring the undoubted Waterberg sandstones are coarse-

BUFFELSHOEK
WARM SPRING

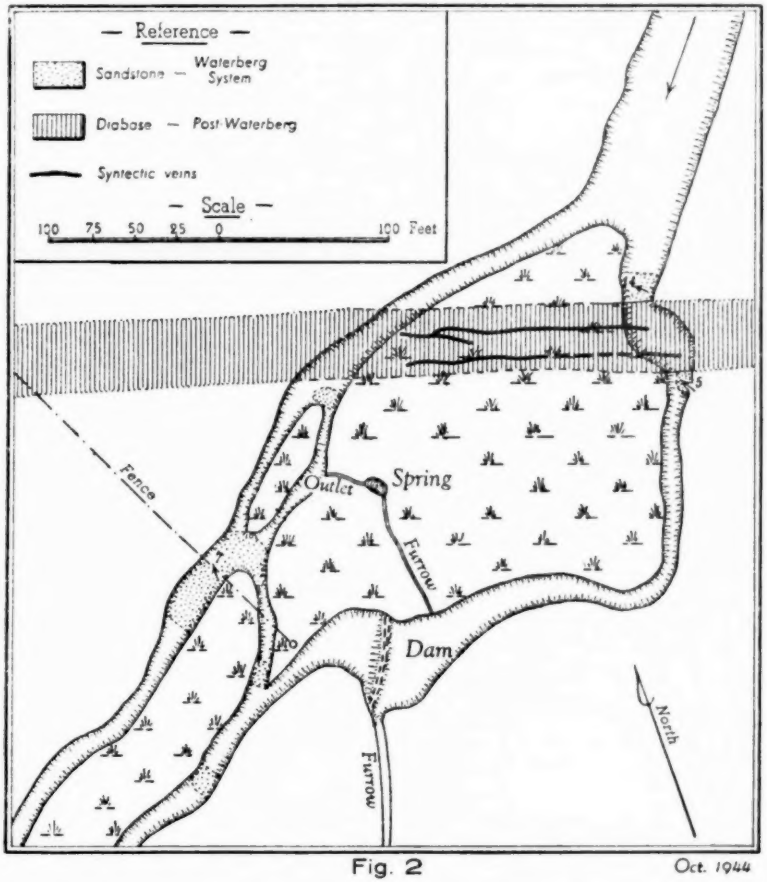


Fig. 2 Oct. 1944

grained and highly feldspathic; in places they could be classed as grits. Small rounded pebbles of white quartzite and vein quartz are fairly common.

The regional dip of the Waterberg beds is to the north-north-east at angles ranging from 3° to 10°. Local variations of dip are common, and

in the neighbourhood of the spring the dip is to the north-north-west at angles of from 5° to 15°.

Intrusive into the rocks of the Waterberg and Transvaal systems are a number of almost vertical diabase dykes which trend more or less east-west. Fifty-eight feet north of the spring is the near edge of one such dyke, 40 feet

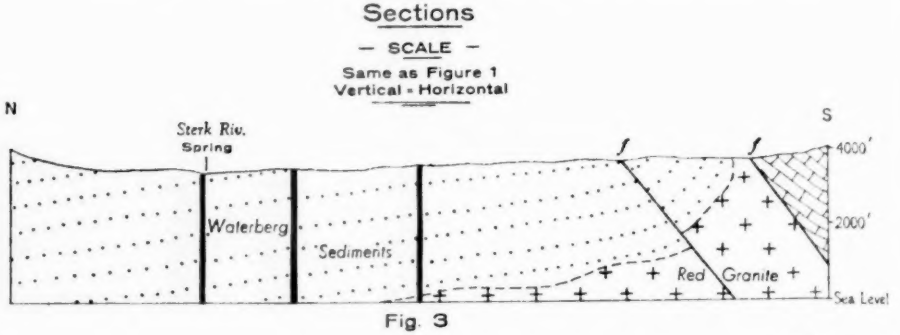


Fig. 3

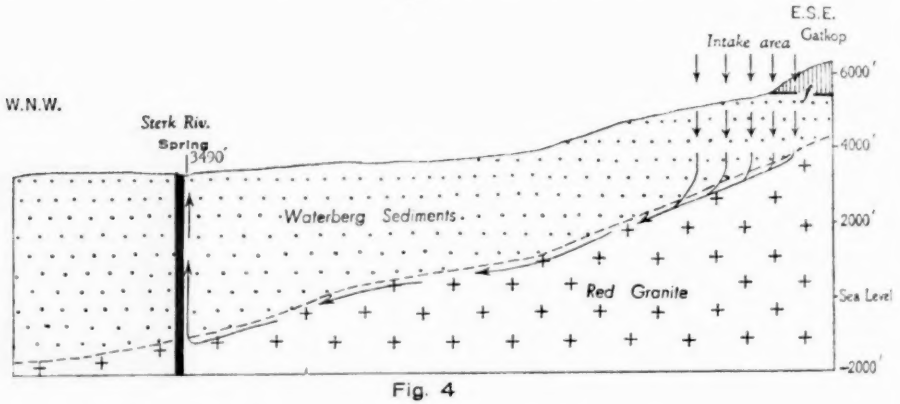


Fig. 4

thick. Of interest are two pale grey, vertically disposed veins, up to 3 inches wide, intruded into the diabase in the manner shown in fig. 2. These veins may represent mobilised Waterberg sediments. The spring dyke and the one to the south of it probably intersect, but west of the tiny pan both are obscured by surface drift.

Although the southern part of the area has undergone intensive compressional faulting, it would seem that the effect has been indirect as far as the origin of the spring is concerned. This faulting has caused rocks of the Dolomite series and Red granite to overlie the lower part of the Waterberg

system as shown in the sections, figs. 3 and 4. The presence of a resistant capping of banded ironstones at Gatkop has, to a very large extent, been responsible for the preservation from erosion of the high-lying Waterberg sandstones and grits which form the intake area of the Buffelshoek spring. These Waterberg sediments were deposited on an extremely uneven floor. Evidence for this is to be found not only in the area under discussion but also in adjoining areas to the east on Donkerpoort 1315 and to the west on Waterval 1316 and McKip Zyn Rand 956.

Origin and Depth of the Spring.

Several factors are responsible for the presence of a thermal spring on Buffelshoek. First and most important there is the dyke, close up against which the warm water rises to the surface of the ground. Although the spring is not actually on the contact it is significant that it issues on the *downstream* side of the dyke. The primary source of the warm water must therefore be sought on high ground lying south of the dyke.

The dyke at the spring and those associated with it have divided the subsurface waters of the area into definite compartments. In one of these are both Gatkop and the thermal spring. Some of the rain falling on this mountain will be absorbed in the well-jointed sandstones and grits of the Waterberg system and, to a lesser extent, in the rocks of the Dolomite series. Percolating slowly downwards the water reaches the underlying Red granite, of which the uppermost portion is likely to be permeable as it was exposed to weathering in pre-Waterberg times. As is shown in the section, fig. 4, migration northwards is assumed along and just below this contact until the dyke is encountered. The water then finds its way to the surface via a fissure or system of fissures in which the flow becomes concentrated.

The assumed intake area on Gatkop is about 1,500 feet above the spring and, even when allowance is made for friction losses, the hydrostatic head would be quite adequate.

One way of testing this theory of origin is to ascertain whether the water in the postulated artesian system would descend to such a depth that it could become sufficiently heated. Unfortunately no geothermal measurements have as yet been made in rocks of the Waterberg system, but assuming that a previous estimate (7) of 220 feet per 1° C. is approximately correct for the geothermal step, then at Buffelshoek the water would have to descend to a depth of approximately 3,000 feet to attain a temperature of 31° C. Some adjustment of this figure is of course necessary to allow for loss of heat during ascent. This, however, is likely to be but a small factor for, in contradistinction to downward percolation, ascent of pressure water in

fissures is rapid. At all events the deduced geological structure is in accord with this rough geothermal estimate.

In composition Buffelshoek spring water is unlike other springs in Waterberg sandstones. For example, the characteristic ions at the Loubad thermal springs (7) are (N/1000) Ca'' 1·33, Mg'' 0·44, and HCO_3' 2·03.

In the Table on p. 173 analyses are given of water from a cold spring and two boreholes in Waterberg sandstone. In addition an analysis is also given of a sample of water collected by Dr. T. Ockerse from the Sterk river about a mile below the thermal spring; it is thus Waterberg run-off water contaminated to some extent by the spring.

These analyses are remarkably alike, and a previous investigation of the Loubad springs (7) showed that even a thermal spring in Waterberg sediments has an essentially similar composition, although somewhat more concentrated.

Buffelshoek spring water is so different that it is quite evident that it must have percolated through rocks of another type before entering the Waterberg sandstone from which it finally emerges at the surface. In composition it bears a close resemblance to the hot water which issues at Warmbaths from a fault in the Red granite. Comparison of analyses (see p. 174) shows that the only really important difference is the high soda alkalinity at Warmbaths. Dr. Wasserstein reported that spectra of the solids obtained from Buffelshoek and Warmbaths water showed a virtual identity in certain diagnostic elements. Reference to Bond's (1) memoir shows that Buffelshoek is a typical Red granite water bearing all the hallmarks thereof, especially the high fluorine and silica contents. Actually Buffelshoek water is even more characteristic of Red granite origin than Warmbaths, where the Ca'' and Mg'' are abnormally low. A peculiarity at Buffelshoek is the high SO_4'', which suggests the presence of pyrite in some of the rocks leached by the water. The iron of the iron sulphate thus formed must have been base exchanged, for say Na', as there is no iron in the water.

The geochemical deductions regarding the origin of the spring therefore agree with the purely geological.

Classification.

(a) *Physical.*—Clear. Warm. Radioactivity undetermined.

(b) *Chemical.*—A dilute, slightly gassy, siliceous chloro-carbonate water. Non-sulphuretted.

Total ionic concentration N/1000, 16·70.

Ionic concentrations of characteristic constituents:

Na' 6·42, Ca'' 1·55, Cl' 3·81, HCO_3' 3·5.

	Cold Spring, Middelfontein 1044 (7).		Borehole, Johannisberg 861.*		Borehole, Melkrivier Hamlet.*		Sterk River, Buffelshoek 1314.	
Sample collected .	29.11.43.		March 1942.		March 1942.		4.4.41.	
Ions.	Mgm. per Litre.	N/1000.	Mgm. per Litre.	N/1000.	Mgm. per Litre.	N/1000.	Mgm. per Litre.	N/1000.
Na' . . .	n.d.		6·0	0·26	3·5	0·15	5·8	0·25
K' . . .	n.d.		0·2	0·01	0·7	0·02	0·9	0·02
Mg'' . . .	n.d.		3·0	0·25	4·3	0·35	1·8	0·15
Ca'' . . .	4·0	0·20	3·0	0·15	5·0	0·25	5·0	0·25
Fe''', Al''' . .	n.d.		n.d.		n.d.		n.d.	
Sum of Cations .	..	..	12·2	0·67	13·5	0·77	13·5	0·67
Cl' . . .	n.d.		7·0	0·20	14·2	0·40	14·2	0·40
F' . . .	n.d.		0·2	0·01	0·15	0·01	0·06	0·003
SO_4'' . . .	n.d.		3·0	0·06	3·8	0·08	5·3	0·11
HCO_3' . . .	24·4	0·40	24·4	0·40	18·3	0·30	12·2	0·20
NO_3' . . .	n.d.		nil		nil		nil	
Sum of Anions .	..	..	34·6	0·67	36·45	0·79	31·76	0·713
Total sum of ions .	..	..	46·8	1·34	49·95	1·56	45·26	1·383
SiO_2 . . .	n.d.		n.d.		n.d.		n.d.	
Total solids at 95° C.	n.d.		28·0		34·0		36·0	
Temporary hardness as $CaCO_3$.	n.d.		20·0		15·0		10·0	
Permanent hardness as $CaCl_2$ . .	n.d.		nil		16·5		11·0	
Alkalinity as Na_2CO_3 . .	n.d.		nil		nil		nil	
pH . . .	7·6		7·15		6·60		6·7	
Specific resistance (ohm cm.) at 60° F. . .	24,840		23,760		34,200		54,000	

Analyst: W. Sunkel, Division of Chemical Services.

* The farm Johannisberg is 106 miles west-north-west of Potgietersrust, while Melkrivier hamlet lies 73 miles north of Xylstroom.

The samples were also collected by Dr. Ockerse. Recalculated according to technological conventions these analyses were included in Bond's (1) recent memoir. They are given here in the ionic form as originally returned by the analyst.

On Chase Palmer's (10) system the 1944 analysis may be expressed as follows (for comparison, analyses of Warmbaths and Loubad water have been added as representative respectively of thermal springs in Red granite and Waterberg sediments):—

Properties.	Buffelshoek.	Warmbaths.	Loubad.
Primary salinity . . .	59·4	49·3	6·8
Primary alkalinity . . .	18·9	35·7	14·1
Secondary alkalinity . .	20·7	12·5	80·3

Primary salinity is caused by the halides and sulphates of the alkalies.
Primary alkalinity is due to alkaline bicarbonates and carbonates.
Secondary alkalinity is the property associated with bicarbonates and carbonates of the alkaline earths.

The water is moderately hard. Total hardness as $CaCO_3$, 90 p.p.m. Permanent hardness nil.

(c) *Medical*:

Pharmacological Properties.—Owing to the high fluorine content of 6·4 p.p.m. the water should not be drunk.
Physio-therapeutic Properties.—Hypotonic.

Comparison with other South African Thermal Springs.

In chemical composition Buffelshoek water strongly resembles that of Warmbaths, the best known spa in the Transvaal.

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THREE METHODS OF GRAPHIC REPRESENTATION OF CHEMICAL ANALYSES OF IGNEOUS ROCKS.

By Arie Poldervaart, M.Sc., Ph.D., University of Cape Town.

(With seven Text-figures.)

(Read September 17, 1947.)

Abstract.

The three methods discussed in the present paper are: (i) a linear variation diagram obtained by plotting oxide percentages against the ratio $\frac{FeO + Fe_2O_3}{MgO + FeO + Fe_2O_3} \times 100$; (ii) a triangular diagram with co-ordinates MgO, FeO, and $(Na_2O + K_2O)$; and (iii) a modified von Wolff diagram, using weight percentages instead of molecular percentages. Analyses of the Karroo and the Bushveld igneous provinces are used as examples, and the implications of the variations shown are discussed.

I. Introduction.

Petrological literature testifies to the many attempts which have been made to depict graphically the chemical variations in suites of igneous rocks. Two linear methods of graphic representation have become especially popular, viz. the plotting of weight percentages of oxides against the percentage of SiO_2, and the plotting of so-called Niggli values against the si value as abscissa. In both methods SiO_2 is taken as the measure of variation, and it is tacitly assumed that there is a regular and constant variation in the percentages of SiO_2 during the crystallisation of magma. In many cases this assumption appears warranted, but especially in the differentiation of basalt magma serious discrepancies may be encountered. Thus the orthodox silica diagrams as used by Harker (1909) and Bowen (1928) have been severely criticised by various authors, *e.g.* Brammall (1933), Krokström (1937), and Wager and Deer (1939).

During a search for more suitable methods of graphically depicting the variations of especially basaltic magmas, the author found the three methods described below particularly useful. Two of these, the one a linear and the other a triangular diagram, were first used by Wager and Deer (1939),

though only for a limited number of analyses. The third method is a modification of the von Wolff diagram (1922), which maintains the essential features of the original von Wolff diagram, but allows for easier and more rapid calculation as a logical sequence to the norm calculation.

II. The Linear Variation Diagram with the Ratio $\frac{FeO + Fe_2O_3}{MgO + FeO + Fe_2O_3} \times 100$ as Abscissa.

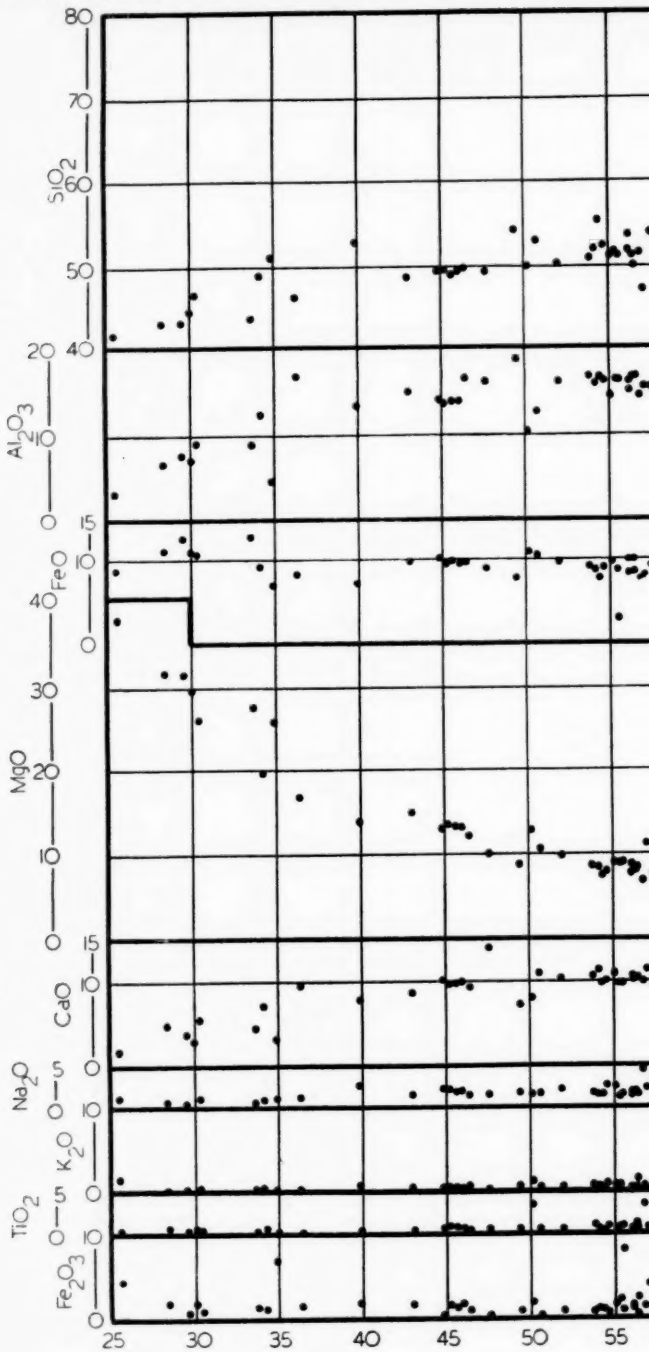
The ratio $\frac{FeO + Fe_2O_3}{MgO + FeO + Fe_2O_3} \times 100$, called here the iron-magnesia ratio, is a particularly useful guide to the variation of those basaltic rocks which are low in ferric iron. The iron-magnesia ratio is a modification of Niggli's mg ratio, or more precisely of the 100(1 – mg) ratio. However, the iron-magnesia ratio is preferred as abscissa, as the calculations necessary for the construction of the variation diagram are simpler, while points on the diagram can be compared directly with the tables of analyses, as weight percentages are used throughout. The minerals separating during the early and middle stages of crystallisation, covering 90 per cent. of the solidification sequence of the original basalt magma, can be conveniently classified into two groups:

(i) Salic minerals, *i.e.* members of the plagioclase series, which show a progressive enrichment in soda during their fractional crystallisation.

(ii) Femic minerals, *i.e.* olivines, pyroxenes, and iron ores, which show progressive enrichment in ($FeO + Fe_2O_3$). This relative or absolute enrichment in iron reaches a peak with the separation of late iron ores, after which it decreases again.

Silica occurs in nearly all the phases separating from the magma, and consequently its variation is the result of a complex balance in the relative proportions and composition of the minerals separating. During the middle stages of crystallisation there is hardly any variation in the percentage of silica. Hence variation diagrams based on the percentage SiO_2 tend to minimise the importance of the middle stages of crystallisation of basalt magma, and to overemphasise the early and late stages of solidification, which are of less significance, both as regards time and volume.

In the competition between the two groups of salic and femic minerals, the variation produced in the magma by the separation of the plagioclase solid solution series is usually stressed. Thus it is generally accepted that continued fractionation of basalt magma will produce a residuum rich in silica, potash, and soda, and hence of "granitic" composition. In keeping with the neglect of the middle stages of crystallisation shown by the



Arie Poldervaart

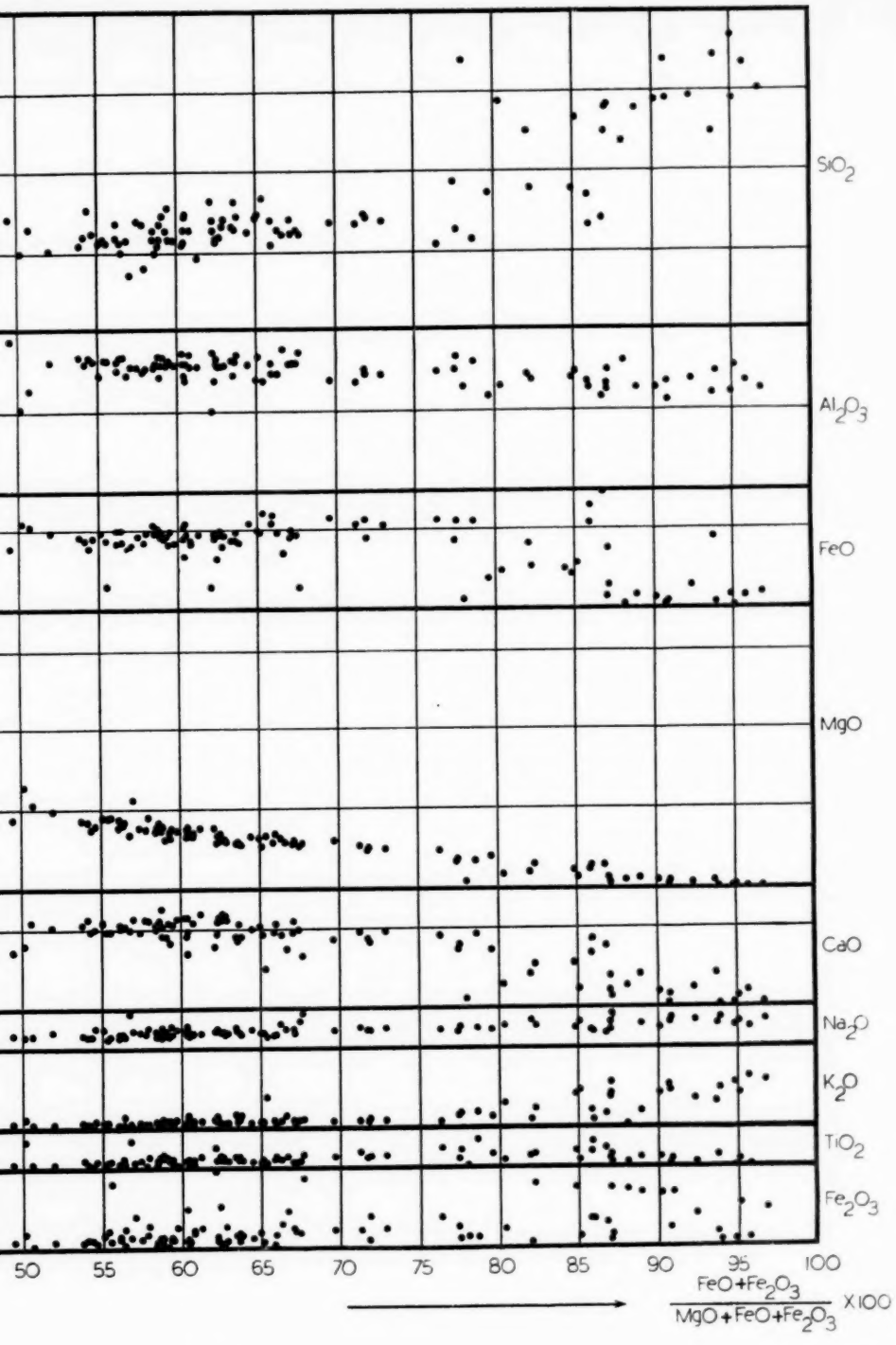


FIG. 1.

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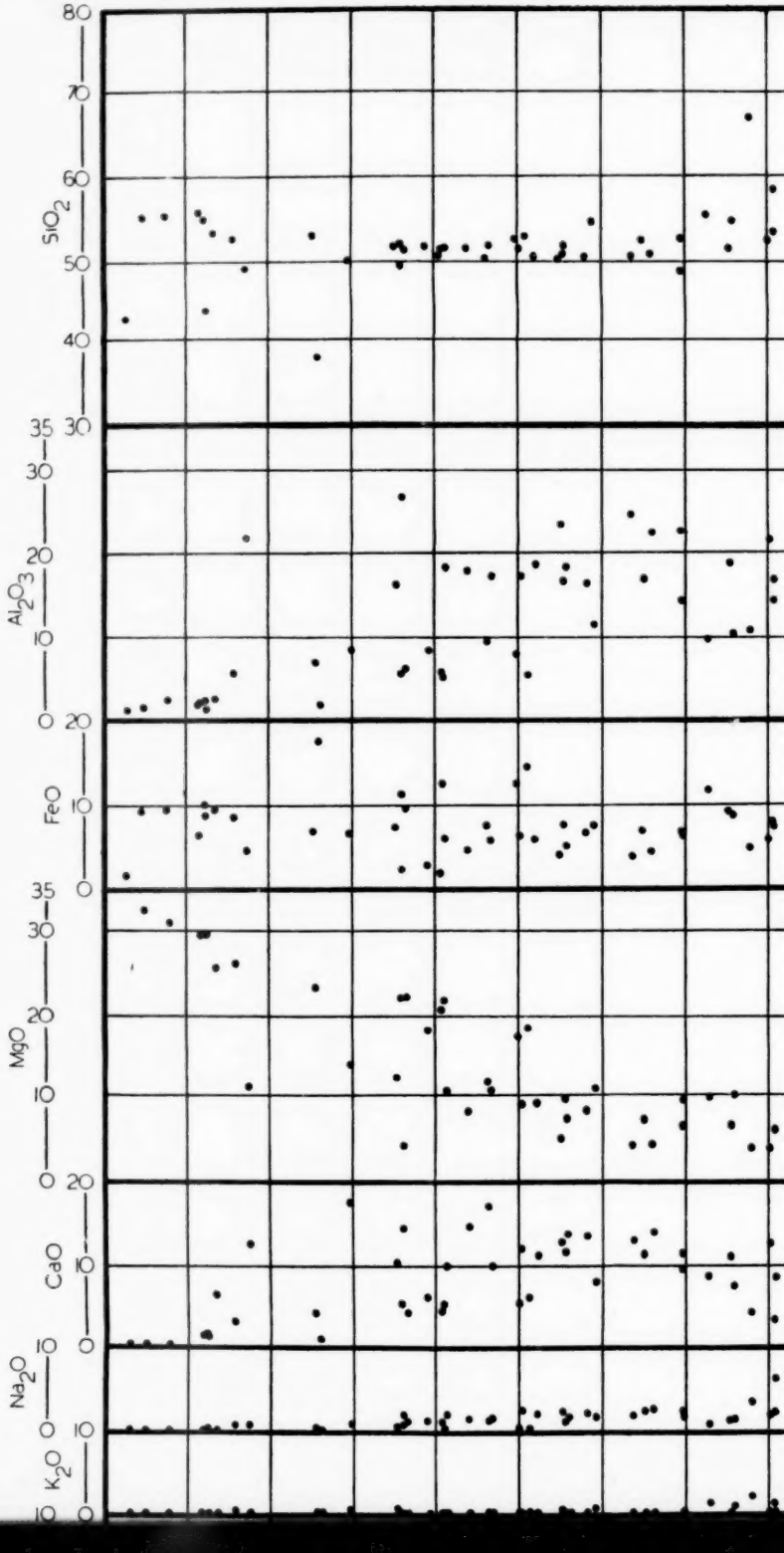
80
70
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SiO_2
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Al_2O_3
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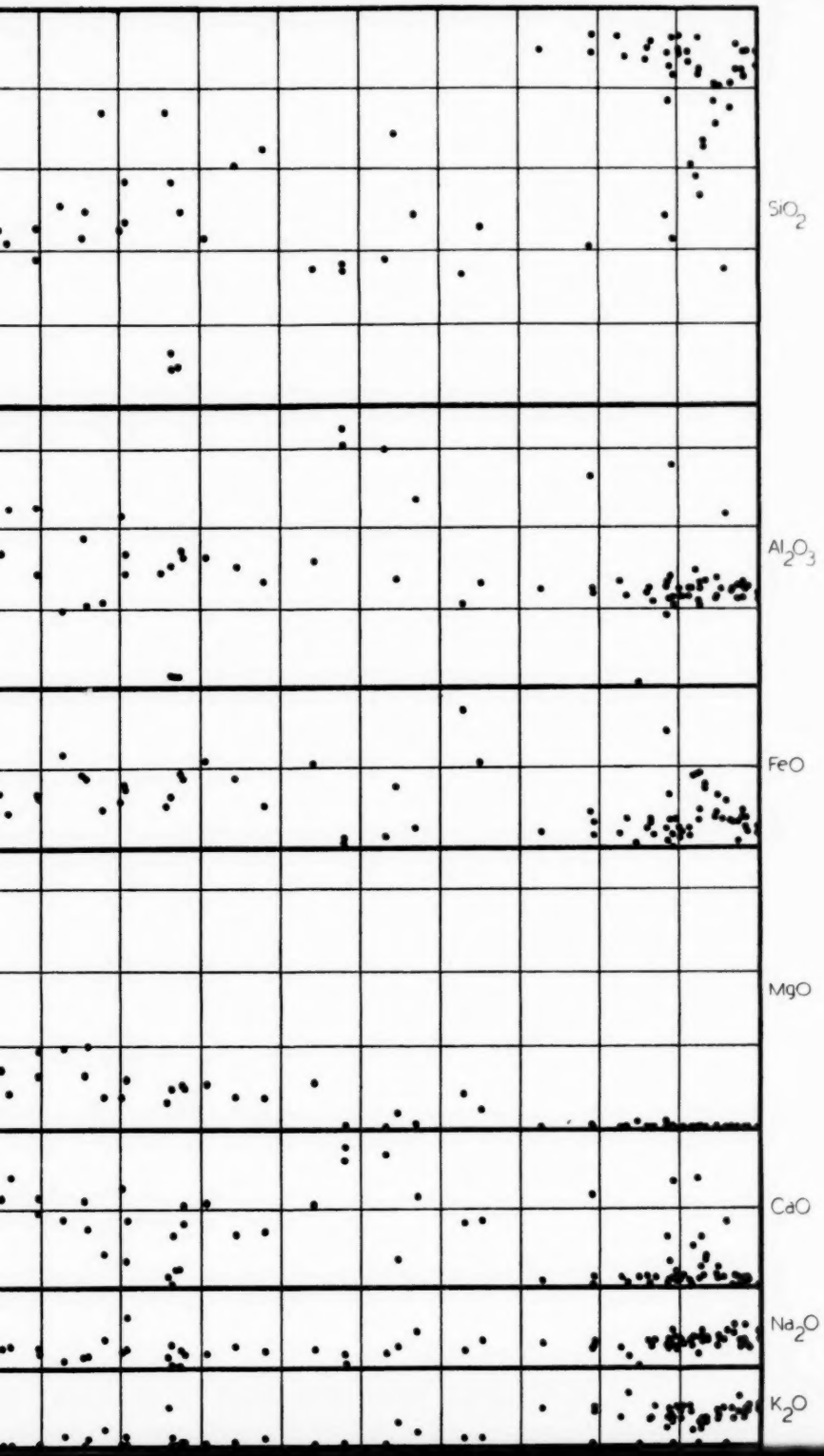
SiO_2
Al_2O_3
FeO
MgO
CaO
Na_2O
K_2O

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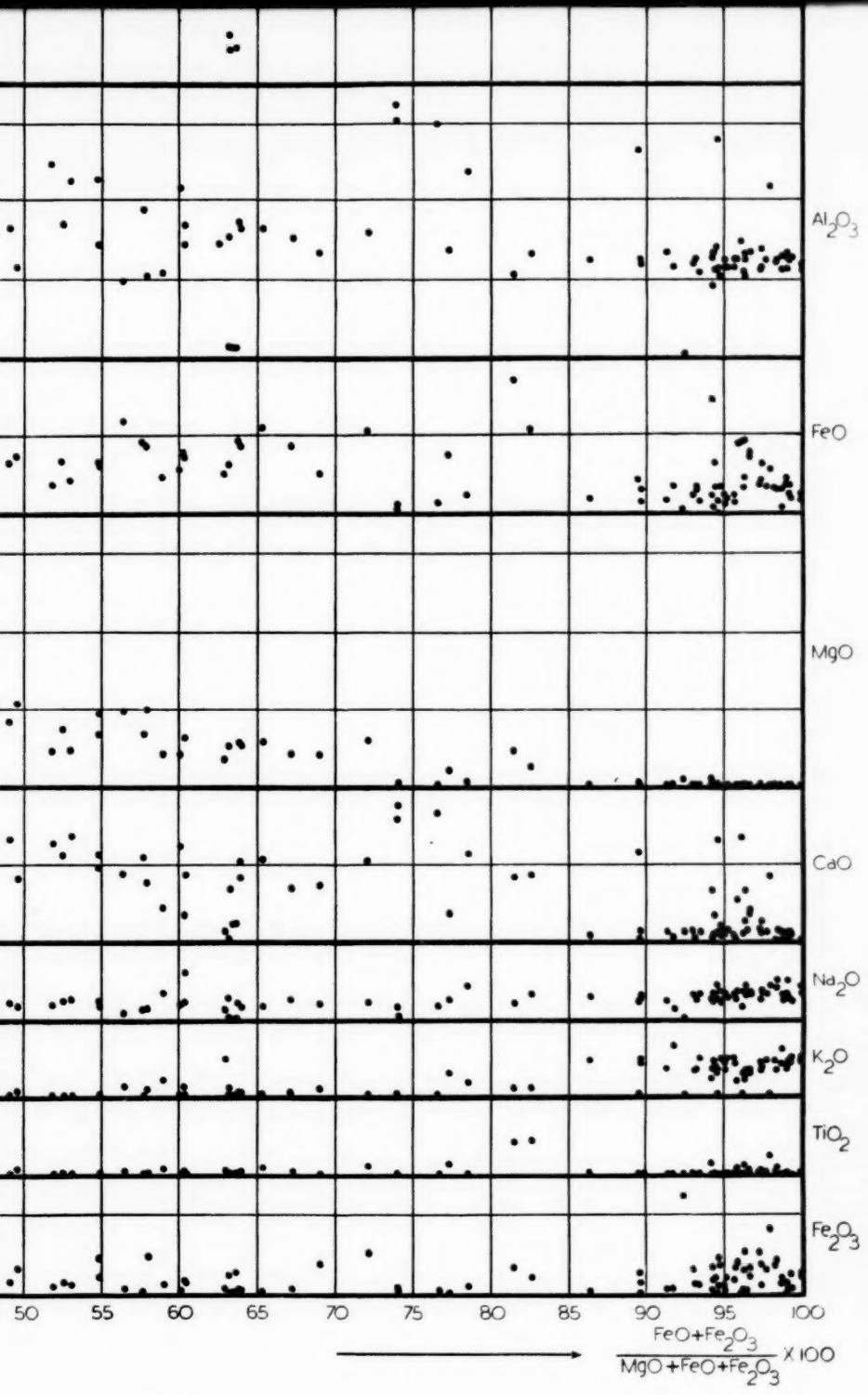

FIG. 2.

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silica variation diagrams, the effects of strong fractionation on the femic group of minerals, in particular the pyroxenes, have been greatly underestimated.

The iron-magnesia variation diagram is especially designed to show the variation during the early and middle stages of crystallisation, and to illustrate the effects of strong fractionation on the femic minerals enumerated above. Like most other linear diagrams, however, this type of diagram is limited in its applicability. Thus it cannot be used for igneous suites with a high Fe_2O_3 content, and becomes a less trustworthy guide when applied to the later stages of crystallisation, during which the variations produced may be attributed chiefly to the group of salic minerals. Since nearly all ferromagnesian minerals have already crystallised when late iron ore separates, the iron-magnesia ratio decreases again during the last stages of crystallisation. Hence the most acid rocks cannot be plotted on this type of diagram.

To illustrate the iron-magnesia variation diagram, 136 analyses of Karroo dolerites (fig. 1) and 109 analyses of rocks from the Bushveld Igneous Complex (fig. 2) were plotted against the iron-magnesia ratio.

The Karroo analyses include all Karroo rocks south of latitude 15° S., *i.e.* the dolerites and lavas of the Karroo Basin proper and the Lebombo belt (Walker and Poldervaart, 1948), the lavas and intrusive rocks from the Kaoko Veld (Reuning, 1929), the lavas and dolerites of Southern Rhodesia (Golding, 1936), and those of the Lupata Gorge (Dixey and Campbell Smith, 1929). For convenience the crystallisation sequence is here divided into three stages, which are discussed in turn:

(i) *Early Stages.*—Iron-magnesia ratio = 25–45. Crystallisation of magnesian olivine and orthopyroxene, augite and bytownite. Conforming to the separation of these minerals, increases are shown in the proportions of SiO_2, Al_2O_3, and CaO, with slight increases in Na_2O and K_2O. Marked decreases are obtained in the curves for MgO and Fe_2O_3, with a less marked decrease in FeO.

(ii) *Middle Stages.*—Iron-magnesia ratio = 45–80. Crystallisation of olivine and orthopyroxene respectively enriched in Fe_2SiO_4 and $FeSiO_3$, subcalcic augite and labradorite. The curves for Al_2O_3, FeO, CaO, and Na_2O remain approximately constant. Increases are shown in the proportions of SiO_2, K_2O, TiO_2, and Fe_2O_3, though in all cases the increase is extremely gradual. The curve for MgO shows a continued decrease, but flattens out towards the abscissa.

(iii) *Later Stages.*—Iron-magnesia ratio = 80–100. Crystallisation of fayalite, eulite (Poldervaart, 1947), ferroaugite, iron ore, intermediate and acid plagioclase, quartz and anorthoclase. A marked increase is shown in the SiO_2 curve, with further increases in the curves of Na_2O and K_2O.

Decreases are found in the proportions of all other constituents. FeO and Fe_2O_3 reach a maximum at approximately a ratio of 85–90, thereafter to decrease sharply. MgO shows a continued decrease to zero. Scattering of points, in particular for SiO_2, FeO, and Fe_2O_3, indicates that the iron-magnesia ratio no longer forms a safe guide to the variation of the more acid rocks.

The Bushveld analyses were chiefly obtained from Hall (1938), and include the ultrabasic, basic, and acid phases of the complex. Only 109 analyses were plotted in fig. 2, as several of the most acid granites and some of the monomineralic phases could not be accommodated in the diagram. On the whole, the points registered in the discussion of the Karroo variation are duplicated in the Bushveld variation diagram. A complication is, however, introduced by the rhythmic layering of the ultrabasic and basic rocks of the Bushveld, giving rise to nearly monomineralic rocks and thereby disturbing the normal distribution of salic and femic minerals. The layering might well be ascribed to convection currents operating in the crystallising magma. The currents so envisaged appear to have been most effective during the close of the early and the start of the middle stages of crystallisation, producing pyroxenites, hortonolite dunites, chromitites, anorthosites, etc. Thus the Bushveld variation diagram shows a considerable scattering of points, in marked contrast to the Karroo diagram.

III. The Triangular $MgO - FeO - (Na_2O + K_2O)$ Diagram.

This diagram provides an amplification of the linear iron-magnesia diagram. It is specially designed to contrast the trends of variation of the calc-alkaline series and those basaltic series which show iron enrichment. The three variables are MgO, the significant constituent of the more refractory minerals; FeO (not including Fe_2O_3), the significant constituent of the medium refractory minerals; and $(Na_2O + K_2O)$, the significant constituents of the less refractory minerals. Hence the diagram further emphasises the competition between the salic and femic groups of minerals during the crystallisation of basalt magma. The final outcome of this competition is the same, *i.e.* the production of a residuum rich in silica, potash, and soda. Consequently the end-point of the trend of differentiation should be near the $(Na_2O + K_2O)$ corner of the diagram, while the starting-point is on or near the $FeO - MgO$ boundary, at approximately $MgO = 80–90$. But during the intermediate stages the liquid line of descent may follow different courses, varying between two clearly defined limits:

(i) In the race between salic and femic minerals the former may predominate, and hence magmatic variation may be influenced chiefly by the

effects of fractionation on the salic minerals. Thus after the crystallisation of magnesian olivine, the liquid line of descent should move directly towards the ($Na_2O + K_2O$) corner of the diagram.

(ii) Alternatively the fractionation of the ferromagnesian minerals may be predominant in the crystallisation of the magma, at least during the middle stages of crystallisation. Consequently the differentiation trend

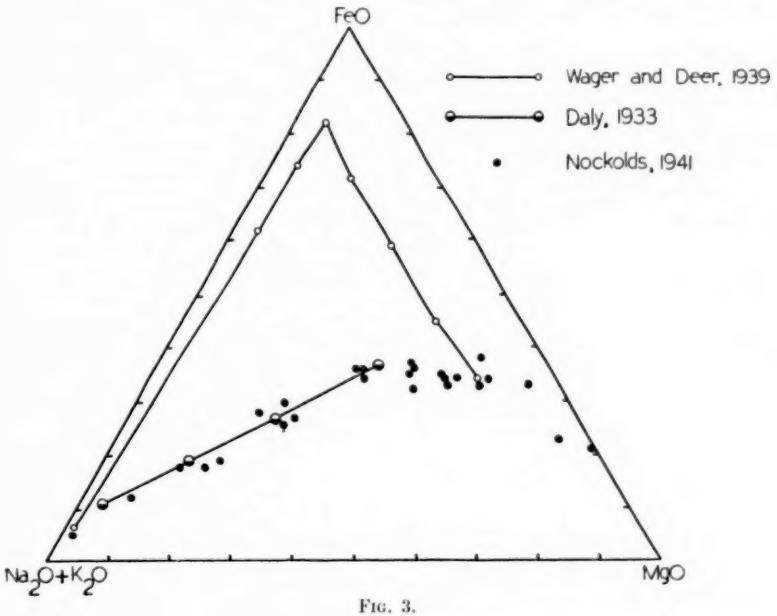


FIG. 3.

should continue to move upwards towards the FeO apex until iron enrichment in the magma has reached a maximum. Thereafter the salic minerals should more strongly influence magmatic variation, since most ferromagnesians have already crystallised. Hence after reaching its maximum the trend should be deflected towards the ($Na_2O + K_2O$) corner, along a course approximately parallel to the $FeO - (Na_2O + K_2O)$ side of the diagram.

The above two extremes are illustrated in fig. 3, which shows Daly's average basalt, andesite, dacite, and rhyolite (1933), and analyses of the Garabal Hill–Glen Fyne Complex (Nockolds, 1941), as examples of the first extreme, while Wager and Deer's Skaergaard line of descent (1939) forms an example of the second type of magmatic variation. In fig. 4 all Karroo

analyses were plotted on this type of diagram. The figure shows that in most Karroo dolerites the influence of fractionation of the ferromagnesian minerals has been stronger than that of the salic minerals. In a few rocks the reverse appears to have been the case, but this may equally well be attributed to late stage processes of albitisation, etc. Hence it may be concluded that during the middle stages of crystallisation of the Karroo

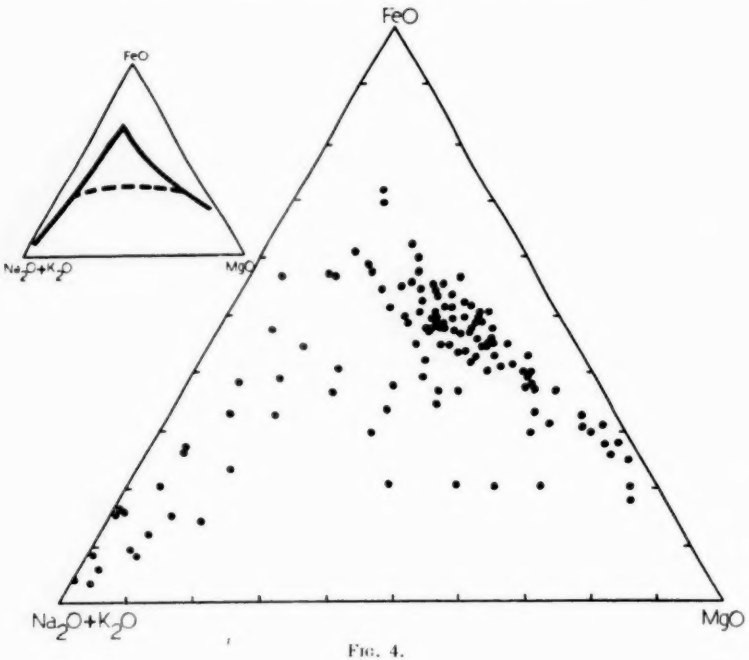


Fig. 4.

magma, fractionation of the ferromagnesian minerals dominated magmatic variation, though iron enrichment was not as pronounced as in the Skaergaard intrusion. The influence of fractionation of the salic minerals only became predominant after the crystallisation of most of the ferromagnesians, when there was a sudden change in the variation trend towards the $(Na_2O + K_2O)$ corner of the diagram.

One hundred and twenty-three Bushveld analyses are plotted in fig. 5. The result, though not entirely unexpected, is remarkable in that both lines of descent are shown in the magmatic variation of the Bushveld magma. This can again be attributed to the rhythmic layering of the lopolith which

produced phases rich in salic, and others rich in femic minerals. In the former, the feldspar line of descent is followed, while the latter show the crystallisation trend of the ferromagnesian minerals. Thus the diagram shows (i) a line towards the FeO apex, which after reaching a maximum turns towards the $(Na_2O + K_2O)$ corner; and (ii) a line from approximately MgO: 35, FeO: 45, $(Na_2O + K_2O)$: 20 towards the $(Na_2O + K_2O)$ corner,

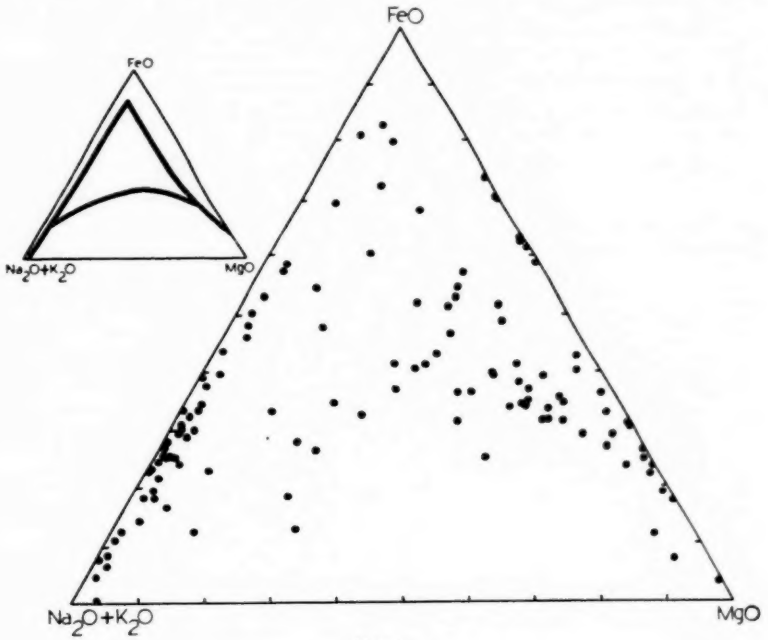


Fig. 5.

corresponding with the calc-alkaline line of descent. In this case it is considered that the second line cannot be attributed to albitisation and allied processes, but that it reflects the fractionation of the salic minerals throughout the crystallisation sequence.

IV. The Modified von Wolff Diagram.

Although von Wolff's method of plotting chemical analyses of igneous rocks was first proposed in 1922, little use has been made of this type of diagram. The only apparent reason for its unpopularity is the rather complicated and tedious calculations involved in plotting the analyses,

necessitating the conversion of weight percentages to molecular proportions and the subsequent recalculation to molecular percentages, after omitting water. Nevertheless Johannsen (1939, p. 109) considered the von Wolff method "a very ingenious method for plotting rock analyses", whereby it is possible to show "not only natural boundaries of rock families which approach those of the mode, but genetic relationships, such as progress of differentiation, crystallisation, and sequence of eruption". Reynolds (1946) used the von Wolff method to illustrate the geochemical changes leading to granitisation, and concluded (1946, p. 393) that "for this purpose the von Wolff diagram is highly suitable, since, on the one hand, it separates quartzose, feldspathic and melanocratic types from one another, and on the other hand, it separates chemically oversaturated rocks from chemically undersaturated rocks". Hence the present author attempted to maintain the essential features of the von Wolff diagram, while seeking to cut down the necessary calculations to a minimum. It appeared logical to base such calculations on the manipulations normally accepted as necessary, *i.e.* the recalculation of the chemical analysis as water-free, to 100 per cent., and the calculation of the norm. Hence the following rules were adopted:—

(i) Recalculate the analysis as water-free, to 100 per cent.

(ii) Convert weight percentages to molecular proportions for each constituent.

(iii) Follow the normal rules for the calculation of the norm, but keeping each normative mineral fully saturated, as if sufficient silica were available to saturate all constituents (*vide* Table I).

TABLE I.

Saturated Normative Minerals used in the Calculations for the von Wolff Diagram.			Undersaturated Normative Minerals (left) calculated as corresponding Saturated Minerals (right).	
Quartz, Zircon	Q	Acmite Na_2SiO_3	Leucite	Orthoclase
Corundum, Orthoclase, Albite, Anorthite	L	Wollastonite	Kaliophilite	Orthoclase
		Enstatite	Nepheline	Albite
		Ferrosillite	Forsterite	Enstatite
		Magnetite	Fayalite	Ferrosillite
		Haematite	Calcium orthosilicate	Wollastonite
	M	Chromite	Perovskite	Titanite
		Ilmenite		
		Titanite		
		Rutile		
		Apatite		

(iv) Allot silica in the usual manner, obtaining a positive value for silica if the rock is saturated, and a negative value if there is insufficient silica to saturate all the minerals.

(v) Determine the percentage weights of the minerals in the usual manner.

(vi) At this stage the co-ordinates for the point on the triangular diagram are found by the following algebraic summations:—

Q = silica (positive or negative) and zircon percentages.

L = percentages of corundum, orthoclase, albite, and anorthite.

M = percentages of all other minerals (*i.e.* acmite, Na_2SiO_3, wollastonite, enstatite, ferrosillite, magnetite, haematite, chromite, ilmenite, titanite, rutile, and apatite).

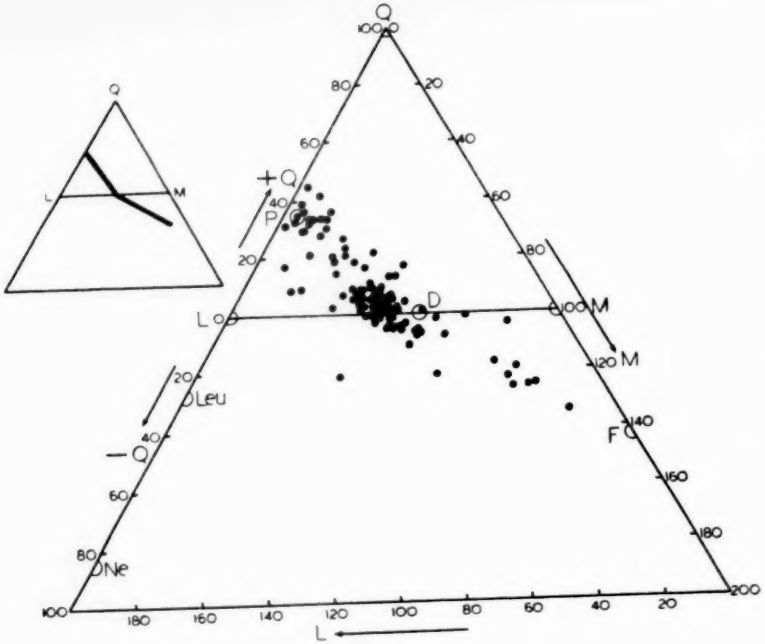
(vii) Having found the values for Q, L, and M, the point is plotted on the triangular diagram: (*a*) if Q is positive above the line L–M, and (*b*) if Q is negative below the line L–M (figs. 6 and 7).

Note.—If the norm calculation shows that the rock is saturated with regard to silica, the summations can be made directly from the norm, and the Q, L, and M values found by recalculation to 100 per cent. In Table II the most significant points of the modified von Wolff diagram are enumerated.

TABLE II.

Point.	Symbol	Q.	L.	M.
Feldspar point	L	0	100	0
Quartz point	Q	100	0	0
Augite point	M	0	0	100
Nepheline point	Ne	−84·5	184·5	0
Leucite point	Leu	−27·6	127·6	0
Forsterite point	F	−42·5	0	142·5
Anorthite-diopside eutectic point .	D	0	42·4	57·6
Daly's average rhyolite . .	P	34·2	61·7	4·1

The von Wolff diagram for the Karroo igneous province (fig. 6) shows the Karroo line of descent starting in the undersaturated field near the forsterite point (F). Thence the course of crystallisation moves upwards towards the saturated field, reaching the saturation boundary L–M at a point to the left of the theoretical anorthite-diopside eutectic point (D). This gives the approximate location of the natural peritectic between labradorite and augite or subcalcic augite. Most dolerite analyses are crowded around the peritectic, indicating that the von Wolff diagram


Q
100
80
20
60
40
60
80
+Q
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P
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100 M
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Leu
140
F
40
−Q
160
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180
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Ne
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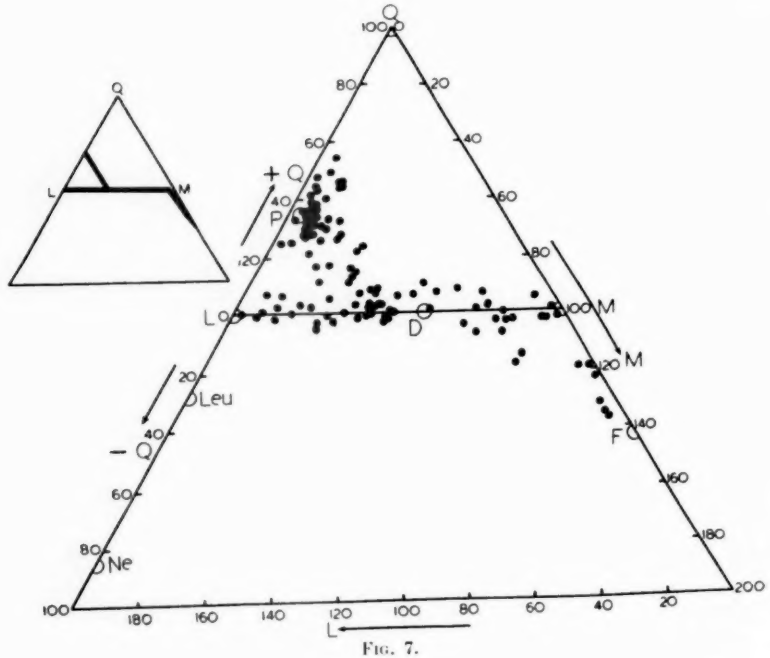
FIG. 6.


Q
100
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−Q
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60
180
80
Ne
100
180
160
140
120
100
80
60
40
20
200
L

FIG. 7.

shares the tendency of the linear silica diagram to minimise the middle stages of crystallisation. The later stages of crystallisation are represented by a line towards the Q–L boundary, which it reaches at approximately Q : 40, L : 60, M : 0, a point which agrees reasonably well with Daly's average rhyolite (P).

Fig. 7 shows the result of plotting the Bushveld analyses by this method. The later stages of crystallisation are the same as those of the Karroo province, but the early and middle stages of crystallisation are markedly different. This must undoubtedly be ascribed to the layering of the ultrabasic and basic phases of the Bushveld magma, producing separate salic and femic rocks. Thus the line of descent climbs steeply from the forsterite point (F) to the augite point (M), and continues from there along the horizontal line M–L. Points to the right of the labradorite-augite peritectic represent rocks consisting essentially of pyroxene, while those to the left of this point (approximately Q : 0, L : 60, M : 40) are the anorthosites. Unfortunately changes in the composition of the feldspars are not shown in the von Wolff diagram, since they all fall together at point L.

V. Conclusions.

The linear iron-magnesia diagram, particularly when used in combination with the triangular $MgO - FeO - (Na_2O + K_2O)$ diagram, is a much more reliable method of depicting the variations of basaltic rocks than the orthodox silica diagram. The latter tends to emphasise the early and late stages of crystallisation, while the middle stages of crystallisation are compressed within a small part of the diagram, due to silica remaining nearly constant during this period in the crystallisation sequence. The products of the middle stages of crystallisation form both in volume and time the greatest part of magmatic consolidation, and hence the silica diagram gives an unnatural picture of the cooling history. The linear iron-magnesia diagram is designed to overcome this obstacle, but its use is limited by the following considerations:—

1. It cannot be applied to rock types rich in ferric iron.
2. The last stages of crystallisation cannot be represented on the diagram, as the iron-magnesia ratio decreases again after the crystallisation of late iron ore.
3. Rhythmic layering, as shown by the Bushveld Lopolith, results in a considerable scattering of points.

The triangular $MgO - FeO - (Na_2O + K_2O)$ diagram overcomes the last two obstacles, but is likewise less reliable when used for rock types rich in ferric iron. The diagram emphasises the important outcome of the

competition between the salic and femic minerals in their influence on the variation of the crystallising magma.

The modified von Wolff diagram provides for quicker and simpler calculation for this type of graphic representation, while preserving all the features of the original von Wolff diagram. Hence it is of general application, but shares the handicap of the original von Wolff diagram in compressing all feldspar and all pyroxene in only two points. Thus the variations in either of these groups of minerals are not shown in the diagram, a disadvantage which is particularly serious in dealing with basaltic rocks.

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THE PARAGENESIS OF A HORNBLENDE LAMPROPHYRE FROM BELLVILLE, NEAR CAPE TOWN.

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(With one Text-figure.)

1. Introduction.

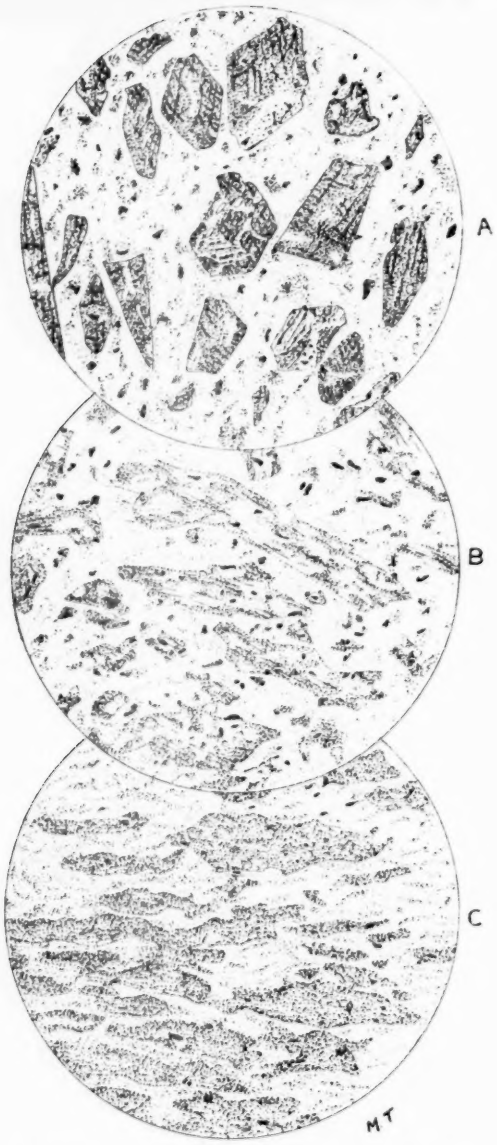
A concordant intrusion of spessartite is exposed in the railway quarries at Bellville, near Cape Town (S. 33° 52′ 40″, E. 18° 37′ 45″), and has been known for several years through the description of Haughton and Rogers.* The intrusion is of a type unique in the district and of an interesting paragenesis. The following account deals principally with the metamorphic history of the rock, and shows how an early phase of thermal metamorphism was succeeded by a later dynamic phase affecting centre and margins differentially. A chemical analysis of the central portion was made with the aid of a grant from the Staff Research Fund of the University of Cape Town, for which grateful acknowledgment is expressed.

2. Field Characters.

The intrusion is injected concordantly into sediments belonging to the pre-Devonian Malmesbury series. In the quarry exposures these sediments are seen to strike roughly N.–S. and to dip to the west at an angle of 70°. They consist of fine-grained siltstone hornfelses rich in biotite, with subordinate slaty bands. The lamprophyre follows one of the latter, which obviously provided a direction of easy parting. In the older portion of the quarries the intrusion is 30 feet thick, but thins out to 8 feet in the north quarry. The continuity of the outcrop is interrupted by faulting.

The lamprophyric character of the centre of the sill is evident in the hand specimen, conspicuous satin-black prisms of hornblende up to 6 mm. in length being embedded in a grey matrix. Towards the margin the hornblende crystals become much less prominent, and the actual contact with the slate is hard to trace.

* Geological Survey of S. Africa, Explanation of Sheet No. 247 (Cape Town), 1933, pp. 37–38.



TEXT-FIG.—Spessartite from Bellville, near Cape Town.

A. Ordinary light, ×38. Central portion of spessartite intrusion in which dark twinned hornblende is prominent.

B. Ordinary light, ×38. Metamorphosed marginal portion of spessartite intrusion containing conspicuous pseudomorphs after hornblende in actinolite (grey) and biotite (black).

C. Ordinary light ×38. Schistose contact portion of spessartite showing elongated and streaky pseudomorphs after hornblende in biotite. Contact is seen at bottom left-hand quadrant.

The intrusion is practically free from xenoliths or ocellar spots, but the central portion contains a number of thin light-coloured veins which do not exceed 5 mm. in width. They appear to be the result of alteration along solution channels.

3. Microscopic Characters.

(a) *Central Portion.*—The central portion of the intrusion has been described by Rogers (*loc. cit.*), who recognised it as a typical spessartite, and there is little to add to his account. The conspicuous prisms of hornblende, which form about 35 per cent. by volume of the rock, reach a maximum size of 6 mm. × 1·5 mm. but average about half these dimensions. They are sharply idiomorphic, and present a marked contrast to the fine-grained and somewhat obscure groundmass in which they are embedded. The usual combination of prism and clinopinacoid is shown with twinning parallel to the orthopinacoid. The optical properties are as follows: –

$\alpha = 1{\cdot}664$	$\gamma - \alpha = 0{\cdot}019$	Pleochroism	α, pale brown
$\beta = 1{\cdot}675$	$2V(-) = 78°$ *		β, greenish brown
$\gamma = 1{\cdot}683$	$\gamma \wedge c = 16°$		c, dark brownish green

Though the orientation of the hornblendes is mainly haphazard there is an occasional tendency towards parallelism (fig. A).

The average grain size of the groundmass is only 0·22 mm. It is highly felsic, consisting largely of a granular aggregate of acid plagioclase with subordinate quartz and orthoclase. It was found impossible to obtain an exact determination of the plagioclase, but it appears to lie within the oligoclase range. Minor constituents, not exceeding one or two per cent. are apatite (in needles coloured grey by inclusions), magnetite, pyrite and chlorite. In addition there are numberless minute needles of pale green or colourless amphibole and more rarely of clinopyroxene, either scattered through the groundmass or as an outgrowth from the margins of the amphibole phenocrysts.

A feature of the central portion of the intrusion is the irregular veining of the hornblende phenocrysts by small unorientated flakes of red-brown biotite. In the light-coloured veins which traverse the rock, hornblende gives place to granular and colourless clinopyroxene up to 0·3 mm. across with $2V(+)$ approximately 50° and $\gamma \wedge c = 40°$. The centre of the veins is frequently occupied by calcite.

A chemical analysis of the central portion of the intrusion was made by W. H. Herdsman and is given below. It shows reasonable agreement with the average spessartite of Johannsen, which is quoted for comparison.

* Kindly determined by Dr. A. Poldervaart.

	I.	II.
SiO_2	55·32	52·85
TiO_2	0·69	1·03
Al_2O_3	15·06	15·74
Fe_2O_3	0·87	3·04
FeO	7·81	4·81
MnO	0·32	0·06
MgO	5·77	6·24
CaO	6·98	7·58
Na_2O	3·13	3·58
K_2O	2·66	2·39
H_2O^+	0·90	2·05
H_2O^-	nil	
P_2O_5	0·29	0·07
CO_2	nil	0·12
	99·80	99·56

Norm of I.		
Quartz		1·00
Orthoclase		16·12
Albite		26·72
Anorthite		18·90
Diopside		11·44
	$CaSiO_3$ 5·80	
	$MgSiO_3$ 3·00	
	$FeSiO_3$ 2·64	
Hypersthene		21·56
	$MgSiO_3$ 11·40	
	$FeSiO_3$ 10·16	
Magnetite		1·39
Ilmenite		1·37
Apatite		0·67
H_2O		0·90
		100·07

Specific gravity of I = 2·88.

I. Centre of spessartite sill, northern end of railway quarry, Bellville, near Cape Town. Analyst, W. H. Herdsman. New analysis.

II. Average of 14 analyses of spessartites. Quoted from A. Johannsen, Igneous Petrography, vol. 3 (Chicago, 1937), p. 192.

(b) *Margins.*—Apart from slight variations in the average dimensions of the hornblende phenocrysts, the central portion of the intrusion is very uniform, but there are marked changes towards the margins, commencing a foot or so from the contact. The first difference observable is in the hornblende phenocrysts, which become altered to small thin prisms of pale green actinolite between which little flakes of red-brown biotite occur abundantly (fig. B). The actinolite crystals are elongated roughly parallel to the original hornblende prisms. At about 1 inch from the contact the intrusion becomes schistose in character. The phenocrysts show increasing parallelism and elongation while actinolite disappears, giving place entirely to red-brown biotite, and the groundmass becomes so obscure as to be indeterminable. Immediately adjacent to the contact the phenocrysts are represented by shapeless streaks of biotite flakes, which become increasingly tenuous and ill-defined (fig. C). The actual contact is clear-cut under the microscope, for the very fine grain of the Malmesbury slate shows a marked contrast to the streaky schistose margin. The streakiness of the contact phase makes it difficult to estimate the amount of chilling, but in places the grain size continues undiminished to less than 1 cm. from the contact. It is possible, indeed, that there was little or no chilling.

4. Paragenesis.

Emplacement.—The intrusion was emplaced concordantly in the Malmesbury series as a single injection before this formation was invaded by the granites of the S.W. Cape. Like the country rock it has suffered mild contact metamorphism by the neighbouring granite, and since the injection of the plutons is known to be intimately connected with the folding of the Malmesbury,* it is at least possible that the lamprophyre was intruded prior to the main diastrophism.

Contact Metamorphism.—The mild contact alteration of the Malmesbury siltstones and slates has resulted in the formation of abundant red-brown biotite. It is believed that the very similar biotite veining the hornblende phenocrysts of the lamprophyre is also a product of contact metamorphism, being developed from chlorite formed as an early alteration product of the amphibole. The abundance of biotite pseudomorphous after hornblende adjacent to the contact is explained by the more complete chloritisation of the contact hornblende.

The minute needles of amphibole and pyroxene in the groundmass and round the peripheries of the phenocrysts are probably other products of contact metamorphism and represent the clearing up of decomposition products. It is thought, further, that the diopsidic clinopyroxene of the light veins in the central phase resulted from the reaction thermally of chlorite with quartz and calcite.

Dynamic Metamorphism.—The intrusion appears to have been affected differentially by dynamic metamorphism subsequent to the intrusion of the S.W. Cape granite. Only thus can the schistose character of the margins be explained. The central portion of the intrusion with its largely unorientated and unaltered hornblende crystals is thought to have offered a successful resistance to shearing stress. The hornblende crystals remained stable through the preceding phase of thermal metamorphism, and tests on road aggregates prove that non-schistose hornblendic rocks have in general great toughness as indicated by high crushing strength and resistance to impact.† The actual values for the crushing strength of the Bellville lamprophyre and micaceous slate are respectively 48,000 and 21,000 lb. per square inch, thus demonstrating the relatively yielding character of the latter. The coarser grain size of the micaceous marginal lamprophyre would render it even more yielding than the adjacent slate, and it is not surprising that a prominent schistosity should have developed together with

* D. L. Scholtz, "The Younger pre-Cambrian Granite Plutons of the Cape Province", Proc. Geol. Soc. S. Afr., 1946, p. lxxx.

† Mem. Geol. Survey, Great Britain, "Attrition Tests of British Road-Stones", 1929, pp. 74–75.

a kind of strain-slip cleavage as evidenced by the miniature thrust faults. The portion intermediate between the central phase and the schistose contacts shows the effects of dynamic metamorphism by developing elongated prisms of actinolite in place of a normal hornblende, but the greater part of the intrusion is unaffected.

A second phase of normal chemical weathering appears to have followed the dynamic metamorphism, but its effects are slight and confined to incipient chloritisation and alteration of the plagioclase.

THE ETIOLOGY OF PELLAGRA. A REVIEW.

By L. Gorfinkel.

To-day there are three theories relating to the etiology of pellagra:

(1) Deficiency of a vitamin identified in 1937 as nicotinic acid.
(2) Deficiency of the amino acid tryptophane in the diet.
(3) The presence of a pellagragenic toxin in maize.

Recent work has indicated that all three theories may together not only explain the production of the disease, but also the relationship between the consumption of maize and the incidence of pellagra.

Pellagra and the Identification of the Pellagra-Preventive Factor.

Pellagra is a disease endemic in those parts of the world where maize constitutes the main food. Casal in 1735 was the first to observe that the incidence of pellagra was associated with the consumption of maize. This relationship though very common is not invariably found.

In 1914 Voegtlin (57) postulated that a deficiency of certain amino acids might be a factor in the incidence of pellagra, and the discovery in recent years of the relationship between tryptophane and nicotinic acid has fully borne out Voegtlin's view. Goldberger and Wheeler (22) definitely showed that pellagra was a food-deficiency disease. In 1920 Chick and Hume (5) reported the production in monkeys of symptoms closely resembling pellagra by the prolonged feeding of a low protein diet, and that the administration of tryptophane to one monkey staved off death for many weeks. Goldberger and Tanner (20) observed some beneficial results when they treated pellagrins with tryptophane and cystine. In 1924 these workers were able to prevent pellagra by incorporating high protein foods such as milk, meat and legumes in the diet (21). Goldberger finally came to the conclusion that the disease was due to the deficiency of a vitamin which he termed the Pellagra-Preventive (P.P.) factor. The search to identify this factor now started. In 1928 Goldberger and Wheeler (23) demonstrated that canine black tongue was analogous to human pellagra, and this finding meant that dogs could now be used as test animals in the search for the cause of the disease.

In view of the newly discovered water-soluble vitamins in liver, Goldberger and Sebrell (19) tested liver extract on dogs with black tongue and found it had a beneficial result. In 1933 Ramsdell and Magness (46) cured 22 cases of pellagra with liver extract. Chick (4) during the same year suggested that pellagra was due neither to the lack of a B vitamin nor to a deficiency of an amino acid, and proposed that the disease was caused by a toxic substance in maize the action of which could be prevented by sufficient protein of high biological value or perhaps by a sufficient supply of a B-complex vitamin. Rhoads and Miller (47) tried to produce black tongue by means of a diet deficient in riboflavin without success, and Elvehjem and Koehn (14) and Birch *et al.* (3) failed to cure it by means of this vitamin. In their work on the effect of liver extract on the pellagra-like condition in chicks, Elvehjem and Koehn (14) prepared a flavin-free fraction which was effective in curing the chicks. Koehn and Elvehjem (35), (36) prepared concentrates of the P.P. factor which proved highly effective in curing dogs with black tongue, but these authors did not succeed in isolating the vitamin. In the meantime, following the report of Warburg and Christian (59) that nicotinamide was the active constituent of co-enzyme II, a deep interest was aroused in the possible role of nicotinic acid in the body. In 1935 Kuhn and Vetter (41) isolated nicotinic acid from heart-muscle, and during 1937 Funk and Funk (18), using pigeons and rats as test animals, reported that nicotinamide and, to a certain extent, nicotinic acid caused a great improvement in appetite and improvement in weight. About the same time Frost and Elvehjem (17) showed a definite growth response in rats on a purified ration when they were fed adenine nucleotides and nicotinic acid. The spotlight was now definitely on nicotinic acid and derivatives of nicotinic acid, and on comparing the properties of nicotinic acid with those observed for the P.P. factor, Elvehjem, Madden, Strong and Woolley (15) immediately recognised similarities and decided to test out pure nicotinic acid on dogs with black tongue. A dog with all the typical symptoms of the disease was dosed with 30 mg. of nicotinic acid and a phenomenal response was obtained. The appetite improved, the mouth lesions disappeared, and the dog started putting on weight rapidly. In this way was nicotinic acid identified as the anti-black tongue factor. Shortly afterwards Elvehjem *et al.* succeeded in isolating the P.P. factor from liver (16).

The results of Woolley and his associates (65) strongly indicated that a highly specific structure was required for curing black tongue. Of seven pyridine derivatives found effective—nicotinic acid, nicotinamide, ethylnicotinate, methylnicotinamide, diethylnicotinamide, nicotinamideglucosidoiodide and nicotinuric acid—all have the α-carbon atom unsubstituted. It was suggested that only those substances which can be converted to

nicotinic acid or nicotinamide in the body possess anti-black tongue activity.

In view of the analogy between canine black tongue and human pellagra, Elvehjem *et al.* (15) suggested that nicotinic acid might be effective in the cure of that disease. Spies and his co-workers (54) soon achieved successful results with nicotinic acid therapy in eleven cases of severe pellagra. Spies observed that the best results were obtained when nicotinic acid was given together with a well-balanced diet, and time has completely justified this view.

Basic Rôle of Nicotinic Acid in Plants and Animals.

Nicotinic acid was first produced by Huber (28) in 1867 by oxidising nicotine with potassium chromate and sulphuric acid. Nicotinic acid is widely distributed in nature in the form of the ubiquitous methyl betaine trigonelline isolated from the plant *Trigonella foenum graecum* by Jahns (30) in 1885. In 1912 nicotinic acid was isolated from rice (55), and fourteen years later Szymanska and Funk (56) attributed to nicotinic acid and nicotinamide a food-sparing and weight-preserving action. Even with this finding nicotinic acid still remained of purely theoretical interest. In 1935 it was the work of Warburg and Christian (58), (59), and von Euler, Albers and Schlenk (13), in identifying nicotinamide as a constituent of co-enzymes I and II that focused considerable attention on the possible rôle of nicotinic acid derivatives in the body.

In both animal and plant tissues nicotinamide is a constituent of co-enzymes I and II. These co-enzymes play an important rôle in cell oxidation-reduction processes. The work of Warburg and Christian (60) demonstrated that it was the nicotinamide unit of co-enzyme II which could accept one hydrogen atom and undergo hydrogenation to the ortho dihydrocompound. In the presence of a suitable hydrogen acceptor such as the yellow respiration enzyme this ortho dihydrocompound could undergo dehydrogenation to its original form. Free nicotinamide could not be hydrogenated to the reversible dihydrocompound, and Karrer *et al.* (31) deduced that nicotinamide was bound in co-enzymes I and II in the form of its quarternary pyridinium salt, and that the reversible hydrogenation property of nicotinamide was related to this type of linkage.

In 1935 Warburg and Christian (59) established that co-enzyme II was constituted by one molecule of nicotinamide, two molecules of a pentose sugar, three molecules of phosphoric acid, and one molecule of adenine. Co-enzyme I differs from co-enzyme II in that it possesses one molecule less of phosphoric acid. Nicotinic acid is required in the body for the synthesis of co-enzymes I and II (25). The exact path of co-enzyme synthesis still remains to be discovered. The view that a nicotinic acid deficiency caused failure of the tissue respiratory mechanism involving

the pyridine nucleotides was not borne out by the work of Handler and Dann (24), whose work pointed to dehydration and electrolyte imbalance as being possibly of primary importance in causing death in the case of nicotinic acid deficiency.

Metabolism of Nicotinic Acid Derivatives.

An excellent review of this subject was given by Ellinger (8). Ingestion of nicotinamide was followed by excretion of N^1-methylchloronicotinamide and small quantities of nicotinic acid and nicotinamide in the human urine. The above derivatives together with trigonelline and nicotinuric acid were found in urine in amounts that varied with the diet. N^1-methylchloronicotinamide is one of the chief end-products of nicotinamide metabolism in the human being (29). It is pointed out that only 15 per cent. of a single dose of nicotinamide is eliminated as N^1-methylchloronicotinamide. Recently Knox and Grossman (32) discovered a new metabolite of nicotinamide in human urine. It would appear that this compound, N^1-methyl-6-pyridone-carboxylamide, is excreted in an amount at least comparable to that of N^1-methylchloronicotinamide. This still leaves 60–70 per cent. of ingested nicotinamide to be accounted for in a balance study. The identification of N^1-methylchloronicotinamide is of practical importance, because pellagra patients excrete much smaller amounts of this metabolite than do normal individuals. (Physically fit persons excrete 6·0 mg., pellagrins 0·45 mg. per day (12)). This led to the establishment of a N^1-methylchloronicotinamide urinary excretion test for the early detection of nicotinic acid deficiency.

The methylation of pyridine in the body was observed by His (27) in 1887. Perlzweig and his associates (45) reported that nicotinamide and not nicotinic acid underwent methylation and that the methylation took place in the liver. Recent work by Ellinger and Hardwick (12) claimed that a portion of the N^1-methylchloronicotinamide produced was eliminated with the bile into the small intestine, where it was destroyed by the intestinal flora. This finding, if substantiated, would account for at least part of the nicotinamide "lost" in the metabolic process.

Biosynthesis of Nicotinic Acid Derivatives.

Nicotinic acid derivatives are synthesised by the intestinal flora (9), (10), (11). Using the "sterilising" drugs sulphaguanidine and succinylsulphathiazole, Ellinger *et al.* (9) reduced the output of urinary N^1-methylchloronicotinamide by 30 per cent. Benesch (2) showed that a suspension of bacteria from the caecum destroyed nicotinamide under anaerobic conditions

and produced it under aerobic conditions. A disturbance in the intestinal tract against the anaerobic bacteria ought to produce an increase in the synthesis of nicotinamide. This was confirmed by the use of ambamide (*p*-aminomethylbenzenesulphonamide), which, being effective against the anaerobic bacteria, brought about an increase in the output of N^1-methylchloronicotinamide. Coulson and Stewart (6) experimented with infants less than two days old and showed that they excreted at least 3·2 mg. N^1-methylchloronicotinamide per 24 hours. This was far more than could have been derived from the amount of nicotinic acid derivatives in the small quantity of breast milk ingested. Najjar and co-workers (44) placed human subjects on a purified diet containing 1·6–2·0 mg. nicotinamide per day. No signs of deficiency developed, and the authors attributed the maintenance of good health and normal excretion of N^1-methylchloronicotinamide to biosynthesis of nicotinamide in the intestine.

Relationship between Nicotinic Acid and Tryptophane.

Wintrobe *et al.* (61) working with pigs demonstrated that when these animals were fed a high protein diet (26·1 per cent. casein), supplemented with all the vitamins except nicotinic acid, they did not develop nicotinic acid deficiency symptoms. On the other hand, when the protein content of the diet was low (10 per cent. casein) the omission of nicotinic acid was associated with marked deficiency symptoms. This pointed to a close relationship between protein and nicotinic acid, and Wintrobe felt that when pigs were fed a diet with a high protein level the dietary requirement of nicotinic acid was somehow altered.

Despite the finding by Dann (7) that the rat was able to synthesise its own nicotinic acid and was therefore independent of a dietary source, Krehl, Tepley and Elvehjem (40) succeeded in producing nicotinic acid deficiency symptoms in this animal by incorporating maize in a synthetic nicotinic acid-free basal ration. They further established that the growth-depressing action of maize could be counteracted by supplying nicotinic acid to the diet. With glucose as the carbohydrate, or when the level of casein was raised to 20 per cent., the growth depression due to maize was diminished. Of striking interest is the fact that when polished rice or rolled oats, which contain less nicotinic acid than maize, were fed under identical conditions they produced no growth depression. Further, milk, although very low in nicotinic acid, was active in combating the deleterious action of maize. The protective action of casein cannot be explained on the basis of its nicotinic acid content, which is low, and Krehl and co-workers (39) soon established that it was the tryptophane content of casein which was the responsible protective factor. This work also explains why milk, which

is low in nicotinic acid but relatively rich in tryptophane, gives protection against the harmful action of maize. The work of Krehl confirmed that the protein level had a profound effect on the nicotinic acid requirement. A diet containing adequate supplies of tryptophane reduces the amount of nicotinic acid necessary to prevent the onset of pellagra symptoms. Krehl and his associates explained the action of maize on the grounds that due to its low nicotinic acid content it sets up an unfavourable set of conditions in the intestinal tract for the synthesis of tryptophane. The reverse is also true. Maize is particularly poor in tryptophane, and the corresponding unfavourable conditions in the intestine reduce the amount of nicotinic acid synthesised by the microflora. Rosen *et al.* (48) showed a significant decrease in the excretion of nicotinic acid derivatives in the rat when the casein of the diet was replaced by gelatin, a tryptophane-deficient protein. On addition of l-tryptophane to the gelatin diet an increased excretion of nicotinic acid occurred within 24 hours. These authors concluded that tryptophane might be the important precursor of nicotinic acid in the rat. Sarett and Goldsmith (51) and Schweigert and his co-workers (53) confirmed these findings. Experiments with the horse (53) offered no indication that nicotinic acid could be converted to tryptophane. Later work by Krehl, de la Huerga and Elvehjem (37) with rats on a synthetic basal diet indicated that addition of nicotinic acid stepped up the utilisation of tryptophane from 30 to 70 per cent. It was stated (37) that it yet remained to be determined whether tryptophane served as the precursor of nicotinic acid in the rat, or whether it simply stimulated nicotinic acid synthesis by the intestinal flora.

The normal metabolism of tryptophane gives rise to kynurenin, kynurenic acid and, as recently discovered by Rosen *et al.* (48), nicotinic acid. In 1943 Lepkovsky, Roboz and Haagen-Smit (42) isolated xanthurenic acid (4-, 8-dihydroxyquinoline-2-carboxylic acid) from the urine of rats kept on a pyridoxine deficient djet, and they established that when l-tryptophane was fed to these rats the excretion of xanthurenic acid was increased. The excretion of this abnormal metabolite stopped when pyridoxine was administered. Lepkovsky *et al.* concluded that pyridoxine was vitally concerned with tryptophane metabolism, and this work was confirmed by Miller and Bauman (43).

The influence of pyridoxine on the conversion of tryptophane to nicotinic acid was investigated (49), (52), and it was shown that rats on a pyridoxine deficient diet were unable to convert appreciable amounts of tryptophane to nicotinic acid. The exact route by which this process proceeds still remains to be determined. Very recent work by Beadle, Mitchell and Nyc (1) suggested that kynurenin was an intermediate in the formation of nicotinic acid from tryptophane by the mould *Neurospora crassa*.

Pellagra-inducing Toxin in Maize.

The old theory of a pellagra-inducing toxin in maize was sharply brought to light by the researches of Woolley (62), (63), (64). His work was based on the competitive theory of analogous substances, *i.e.* a structural analogue of nicotinic acid would compete for the place of nicotinic acid in an active enzyme system but would be quite unable to fulfil the functions of the vitamin. This would then result in the development of characteristic nicotinic acid deficiency symptoms. Woolley showed that 3-acetylpyridine caused a disease in mice (like rats normally independent of a dietary source of nicotinic acid) with the characteristic deficiency symptoms of pellagra. Administration of nicotinic acid or tryptophane to the 3-acetylpyridine-containing diet cured the test animals. Woolley (63) offered the attractive hypothesis that the pellagragenic action of maize might be due to the presence in it of a structural analogue of nicotinic acid which competes with that vitamin just as 3-acetylpyridine does. In a later paper (64) he examined maize for the presence of a pellagragenic substance. From a sodium hydroxide-chloroform extract of maize, Woolley succeeded in preparing a concentrate of a substance which induced severe pellagra-like symptoms in mice. Unfortunately Woolley failed to isolate and identify the substance, but his work was a striking advance in the quest for a pellagra-inducing toxin in maize.

Maize is a rich source of the plant auxin indole-3-acetic acid, and in 1946 Kodicek, Carpenter and Harris (33) reported that indole-3-acetic acid brought about a severe depression in growth of rats. When affected rats were dosed with nicotinic acid or tryptophane they recovered. On a high protein diet indole-3-acetic acid did not produce a depression in growth. These results of Kodicek *et al.* were not confirmed by Krehl and his co workers (38), Rosen and Perlzweig (50), and Henderson and his associates (26). In their latest paper Kodicek, Carpenter and Harris (34) reported that they were unable to repeat their earlier findings with indole-3-acetic acid.

Maize is very poor in tryptophane and low in nicotinic acid, and it appears that pellagra may develop where a condition like this exists in a natural diet.

In the light of the foregoing account the selection and breeding of maize varieties with a high nicotinic acid content is of importance. A report of the author's work in this field appears in The Journal of Agricultural Science, 1948, **38,** 339.

SUMMARY.

Three theories relating to the cause of pellagra have been reviewed and certain interrelationships discussed.

Whereas lack of nicotinic acid was for some time regarded as the main factor in pellagra, recent investigations have revealed that tryptophane also plays an important part. Maize is very poor in tryptophane and low in nicotinic acid, and it seems that pellagra may develop where such a condition exists in a natural diet.

A pellagragenic toxin in maize has not yet been identified.

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PRESSURE GRADIENT ASSOCIATED WITH STEEPLY INCLINED AIR-FLOW.

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(With two Text-figures.)

Abstract.

Steeply inclined air-flow, such as the flow over an escarpment, is of great importance in meteorology. The horizontal pressure field associated with such flow is investigated, and three components, associated respectively with hydrostatic effects, with accelerations and with friction, are evaluated.

A suggestion for the relation between the hydrostatic and the accelerational components is given. The upper-level pressure gradient in the direction of flow is thus calculable from a simple formula, involving the height of the escarpment (or other obstacle), the lapse rate of the air and the temperature.

Application of the theory to practical forecasting is briefly discussed.

Introduction.

The flow of air up or down escarpments or mountain slopes is often of the greatest importance in meteorology. In South Africa, for example, a great plateau is separated from a relatively narrow coastal strip by a steep escarpment. The height of the escarpment varies considerably, but is roughly 3000 feet for long stretches. Air from the ocean may or may not climb the escarpment. Air flowing over the plateau may continue at high level over the sea, or it may subside on to the coast, producing the hot, dry "berg wind". Similar phenomena occur in other countries (*e.g.* the well-known föhn wind), and the investigation of the field of pressure associated with such steeply inclined air-flow is of general interest.

Nature of the Flow.

The flow will first be treated as though it were streamline, later the modifications necessary for turbulent flow (which is far more likely to take place) will be considered. The scale of the motion is such that

the effects of hydrostatic pressure differences, of local accelerations and of eddy-friction are important. These three effects will be discussed and an attempt made to estimate the total pressure gradient associated with the sloping flow. Steady motion is assumed.

Effect of the Coriolis Forces.

These have been neglected in the treatment given below. The coriolis forces always act at right angles to the momentary velocity of the air-parcels. They do not therefore in themselves affect the kinetic energy or the pressure gradient as discussed here, but cause lateral deviations of the air-currents only. If the directions AB and CB of fig. 2 are taken along the direction of air-flow (which is, in general, curved on the chart), then no error is introduced into the calculation of the upper-level field by neglecting coriolis effects. Of course, only by considering these effects is it possible to calculate the actual trajectory of the air.

Hydrostatic Pressure Differences.

AB and CD represent two neighbouring streamlines, with points B and C at the same horizontal level, and AC vertical (fig. 1). The lapse rate of temperature along AC will in stable air be considerably less than the adiabatic.

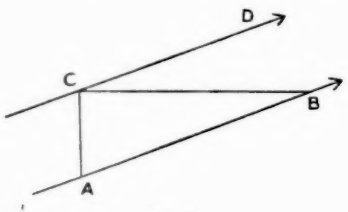

Fig. 1.

Along AB, if the rate of flow is appreciable, the temperature will fall very nearly at the adiabatic lapse rate. Hence B is colder than C, and each point in AB colder than the air at the same level in AC. Consequently, ignoring other effects for the time being, column AB is denser than air column AC, and the pressure at B will be lower than at C. Now B and C are at the same level, and so, to make the pressure single-valued, other forces in addition to the hydrostatic must be invoked. The hydrostatic pressure difference between B and C, together with the effect of local acceleration, will now be evaluated.

Hydrostatic and Acceleration Pressure Effects.

Let A be a point (fig. 2) in the same line of flow as B, as shown, with C vertically above A and at the horizontal level of B. The whole streamline should be far enough above the surface for the effects of minor surface

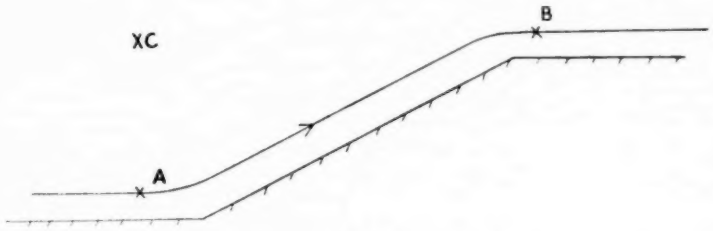

Fig. 2.

irregularities of form and of temperature to be neglected. The lapse rate of temperature between A and C is Γ_1 and that between A and B is Γ—adiabatic or nearly adiabatic. For steady flow we have, using the usual pressure-height relationship for a constant lapse of temperature with height, that pressure at C is

$$P_C = P_A\left(1 - \frac{\Gamma_1 H}{T_0}\right)^{g/R\Gamma_1}.$$

A is chosen far enough from the foot of the escarpment for vertical accelerations along AC to be negligible.

Here H is the vertical height of level BC above A, T_0 is the absolute temperature at A, and R is the gas constant for air. Now $\Gamma_1 H/T_0$ is much smaller than unity for heights of about a kilometre, hence, approximately,

$$P_C = P_A\left[1 - \frac{gH}{RT_0} + \frac{g}{R\Gamma_1}\left(\frac{g}{R\Gamma_1} - 1\right)\frac{\Gamma_1^2 H^2}{2T_0^2} \cdots\right]. \qquad (1)$$

To find P_B, the pressure at B, the acceleration of the air along the streamline must be taken into account. Using the usual notation,

$$\frac{dP}{dz} = \frac{\partial P}{\partial z} + \frac{\partial P}{\partial s}\frac{ds}{dz},$$

where s is the distance along the streamline, *i.e.*

$$\frac{dP}{dz} = -\rho\left(g + \frac{dw}{dt} + \frac{dv}{dt}\frac{ds}{dz}\right),$$

v being the horizontal component of velocity along the streamline and w the vertical component.

Hence

$$\frac{dP}{P} = -\frac{1}{RT}\left\{g + \frac{dw}{dt} + \frac{dv}{dt}\cdot\frac{1}{\tan\beta}\right\}dz,$$

where β is the inclination of the streamline from the horizontal, *i.e.* $\tan\beta = dz/ds$. Now $T = T_0 - \Gamma z$. Integrating and making $P = P_A$ when $z = 0$ and $T = T_0$, we find

$$P_B = P_A\left(1 - \Gamma z/T_0\right)^{\frac{1}{\Gamma R}\left\{g + \frac{dw}{dt} + \frac{dv}{dt}\cdot\frac{1}{\tan\beta}\right\}_{\text{Mean}}}$$

The quantity in brackets in the index is given a mean value. g is nearly constant and the other terms are actually small correction terms, and so the exact method of weighting used to determine the "mean" is not critical, particularly as ρ does not vary very much for the heights considered. As w, the vertical component of velocity, is zero or small both at A and B, the mean value of $\dfrac{dw}{dt}$ may be taken as very small.

Again, if $\bar{v}$ be the mean velocity between A and B and Δv the gain in velocity, then

$$\left(\frac{dv}{dt}\right)_{\text{Mean}} \approx \frac{\Delta v}{\text{time of flow}} \approx \frac{\bar{v}.\Delta v.\beta}{H}$$

for slopes of the order of 1 in 50, or somewhat steeper.

$$\therefore\ P_B = P_A\left(1 - \frac{\Gamma H}{T_0}\right)^{\frac{1}{\Gamma R}\left(g + \frac{\bar{v}\Delta v}{H}\right)},$$

writing H for height z, or

$$P_B = P_A\left(1 - \frac{\Gamma H}{T_0}\right)^{\frac{g+\Delta g}{\Gamma R}}, \qquad . \quad . \quad . \quad \text{(II)}$$

where

$$\Delta g = \left\{\frac{dw}{dt} + \frac{dv}{dt}\cdot\frac{1}{\tan\beta}\right\}_{\text{Mean}} \approx \frac{\bar{v}\Delta v}{H}.$$

For typical values of the various quantities, e.g. $\bar{v} = 10^3$ cm./sec., about 22 miles per hour; $\Delta v = 5 \times 10^2$ cm./sec.; $H = 10^5$ cm. or about 3300 feet; Δg is nearly 5 cm./sec.^{2}, *i.e.* the accelerational forces can be taken into account by a small addition of roughly $\frac{1}{2}$ per cent. to the value of g.

Clearly, if the disturbance is to smooth out at great heights above the escarpment or mountain range, the stream-tubes must tend to smaller vertical thickness at higher elevation. This, combined with a smaller density, requires that the velocity should increase with height, and hence Δv and Δg are positive.

Expanding equation (II) gives

$$P_B = P_A\left[1 - \frac{(g+\Delta g)H}{RT_0} + \frac{g+\Delta g}{R\Gamma}\left(\frac{(g+\Delta g)}{R\Gamma} - 1\right)\frac{\Gamma^2 H^2}{2T_0^2} \cdots\right].$$

Subtracting this from equation (I) we get, omitting higher powers of Δg as small in comparison with the first multiplied by g:

$$P_C - P_B = P_A\left[\frac{\Delta g \,.\, H}{RT_0} - \frac{g\Delta g H^2}{R^2 T_0^2} + \frac{gH^2}{2RT_0^2}(\Gamma - \Gamma_1) + \frac{\Delta g \Gamma H^2}{2RT_0^2}\right].$$

If ρ_0 is the density at A, then

$$P_C - P_B = \rho_0 H\left[\frac{gH}{T_0}\left(\frac{\Gamma - \Gamma_1}{2} - \frac{\Delta g}{R}\right) + \Delta g\left(1 + \frac{\Gamma H}{2T_0}\right)\right].$$

Taking typical values, e.g. $H = 10^5$ cm.; $\Gamma = 10^{-4}$ °C./cm.; $\Gamma_1 = 7 \times 10^{-5}$ °C./cm.; $\Delta g = 5$ cm./sec.^{2}; $R = 2{\cdot}87 \times 10^6$ ergs/gm./°C., it appears that $\Gamma H/2T_0$ is negligible in comparison with unity.

Hence

$$P_C - P_B = \rho_0 H\left[\frac{gH}{T_0}\left(\frac{\Gamma - \Gamma_1}{2} - \frac{\Delta g}{R}\right) + \Delta g\right] \text{dynes/sq. cm.} \quad . \qquad \text{(III)}$$

This represents the upper-level pressure difference necessary for sea-air, for example, to climb a plateau of height H. The major term is the one in $(\Gamma - \Gamma_1)$, showing the importance of the lapse rate.

Discussion of Equation (III).

The term $\dfrac{\rho_0 g H^2}{T_0}\left(\dfrac{\Gamma - \Gamma_1}{2} - \dfrac{\Delta g}{R}\right)$ represents the hydrostatic component of the pressure difference, with $\Delta g/R$ some eight times smaller than $(\Gamma - \Gamma_1)/2$. The acceleration pressure affects $(P_C - P_B)$ in three ways: (i) The rate of fall of pressure with height is not exactly at the same rate as in still air, hence the value of Γ will be very slightly different from the "dry adiabatic lapse rate"; (ii) the accelerational pressure alters the density of the air in column AB and so affects the hydrostatic pressure difference between A and B (this is why the term $\Delta g/R$ appears in the hydrostatic component of the pressure difference); and (iii) the accelerations of the air in column AB are associated directly with pressure differences, which are represented by the contribution of the term $\rho_0 H \Delta g$ to $(P_C - P_B)$.

The complete solution of the problem of the inclined flow of a compressible fluid is difficult, particularly for finite displacements. A rigid determination of Δg in terms of the height of the escarpment, the lapse rate

of the air and the other quantities involved, will therefore not be attempted here. The following simplification is put forward as a suggestion.

Consider a stream-tube forming one of the whole system of tubes. As the tube climbs, the velocity of the air flowing through it is related to the vertical cross-section of the tube. If the velocity of the air increases greatly, the stream-tube becomes very narrow vertically, because the same mass of air must pass every point of the stream-tube per second. Such a vertical shrinking of the stream-tubes towards the top of the escarpment implies that the disturbance dies down rapidly with height above the obstruction. However, a greater amount of energy must be given to the air to provide the kinetic energy associated with the increased velocity. It appears that very large values of the accelerations (*i.e.* of $\Delta g/R$) involve a large expenditure of energy to make the air in the whole system flow over the obstruction. On the other hand, if there is only a small increase in velocity, the stream-tubes will not shrink much and the disturbance will extend far up into the atmosphere. Energy must be given to the air (when initially stably layered) to bring about the inclination of the lines of flow, and an excessive amount of energy will again be necessary if the disturbance extends to great heights. It appears likely, therefore, that for the flow to take place with a minimum expenditure of energy some intermediate value of the acceleration will be appropriate.

It can be seen that a kind of balance is actually set up between the hydrostatic and the accelerational forces associated with the disturbance. The inclination of the streamlines from the horizontal, in air originally stably layered, means that the surfaces of constant density are also inclined. This introduces a set of forces tending to reduce the inclination of the lines of flow. This in turn "compresses" the upper portions of the stream-tubes and necessitates increased velocity of the air. The increased velocity causes the air to tend to overshoot and so to raise the upper portion of the stream-tube and increase the inclination of the system of streamlines. A balance must be set up between these two sets of forces, and the simplest suggestion is that the two terms $\frac{gH}{T_0}\left(\frac{\Gamma-\Gamma_1}{2}-\frac{\Delta g}{R}\right)$ and Δg, which represent the two sets of forces respectively, should be equal. This is supported by the fact that the typical values of the various quantities given earlier actually do make the two terms nearly equal. It has commonly been found by aircraft pilots that in fresh winds the disturbance in the airflow due to mountain ranges or escarpments extends to about $1\frac{1}{2}$ times the vertical height of the obstacle. The increase of velocity with height required by such observations is not inconsistent with the suggestion made above.

The suggestion that the hydrostatic and accelerational terms are equal

is used below to simplify the formulæ for the upper-level pressure field. No proof that the terms are, in fact, equal has been found. Consequently the formulae will also be given in full, with the simplification omitted. This makes

$$\frac{gH}{T_0}\left(\frac{\Gamma-\Gamma_1}{2}-\frac{\Delta g}{R}\right)=\Delta g,$$

$$\Delta g=\frac{RgH(\Gamma-\Gamma_1)}{2(RT_0+gH)}.$$

Substitution of this value makes

$$\frac{\Gamma-\Gamma_1}{2}-\frac{\Delta g}{R}=\frac{\Gamma-\Gamma_1}{2}\cdot\frac{RT_0}{(gH+RT_0)},$$

and from (III):

$$P_C-P_B=\frac{\rho_0 gH^2}{T_0}(\Gamma-\Gamma_1)\cdot\frac{RT_0}{gH+RT_0}. \quad . \quad . \quad \text{(IV)}$$

For rough computation, errors of about 10 per cent. are not excessive, and the factor $\frac{RT_0}{gH+RT_0}$ can be taken as unity for heights of up to 1 km. Then

$$P_C-P_B\approx\frac{\rho_0 gH^2}{T_0}(\Gamma-\Gamma_1).$$

Within a few thousand feet of M.S.L. $\rho_0 g$ is nearly unity, and then

$$P_C-P_B\approx\frac{H^2}{T_0}(\Gamma-\Gamma_1). \quad . \quad . \quad . \quad . \quad \text{(V)}$$

For $H=1$ km., $\Gamma-\Gamma_1=3\times10^{-5}$ °C./cm., and $T_0=3\times10^2$, as before, we get a pressure difference of approximately 1000 dynes/sq. cm. or 1 mb. By way of comparison, it has been observed by many South African forecasters that a pressure difference of at least 1 mb. at 1200 g.d.m. between Durban and Pretoria (4500 ft.) is required to bring sea air into the Transvaal by way of the Limpopo Valley.

Equation (IV) may be compared with a similar result found by the writer for unaccelerated air flowing under the control of coriolis forces (Schaffer, 1946). For saturated air the wet adiabatic lapse rate should be substituted for Γ, otherwise the same calculation applies. When the actual lapse rate Γ_1 is nearly equal to the adiabatic, the resistance to turbulence and to convection becomes much smaller and it is probable that a different kind of flow will result.

Frictional Component.

This will vary with the wind speed and with the coefficient of eddy-viscosity. The coefficient will depend upon the lapse rate, the wind shear, the roughness of the surface and the height above the ground. Clearly the pressure difference $(P_C - P_B)$ of fig. 2 required to overcome friction will change sign if the wind direction is reversed, whereas the pressure difference associated with the hydrostatic and accelerational components is independent of the direction of the wind.

Because of the difficulty in assessing the coefficients of eddy-viscosity over a range of levels, no attempt will be made here to find the exact value of the frictional component by direct means. Instead, a rough calculation based on an assumed angle of cross-isobar flow will be used to give the order of magnitude of the component. It will be assumed that the frictional forces acting on air flowing up or down the slope are the same as if air with the same lapse rate were flowing at the same speed over a horizontal surface of equal roughness. Allowance can then be made for the probable increase of turbulence when the flow is inclined.

With sufficient accuracy for the purpose, we may write

$$\left|\frac{\partial P}{\partial n}\right| = 2v\rho\omega \sin \phi = \rho l v,$$

where $\frac{\partial P}{\partial n}$ is the pressure gradient, v the horizontal wind velocity, and l is written for $2\omega \sin \phi$.

Suppose now that the wind blows across the isobars at a small angle θ. Then, for every centimetre of path length, the pressure on an air-parcel will fall by an amount $\frac{\partial P}{\partial n} \sin \theta$ dynes/sq. cm., and the fall of pressure for length L of path will be $L \sin \theta \frac{\partial P}{\partial n}$.

If friction is unchanged when moving along the slope, then in travelling a distance L the air-parcel will have climbed a vertical distance $L \sin \beta$, where β is the angle of slope. Hence the change of pressure associated with friction will be $\frac{L \sin \theta}{L \sin \beta} \frac{\partial P}{\partial n} \approx \frac{\theta}{\beta} \rho v l$ dynes/sq. cm. per cm. climbed vertically. Hence fall of pressure associated with friction during flow over a slope of vertical height H will be $\frac{\theta}{\beta} \cdot \frac{lv\rho}{10^3} \cdot H$ millibars.

$$\Delta P \text{ (friction)} = \frac{\theta}{\beta} \rho v l H \text{ dynes/sq. cm.} \quad . \quad . \quad \text{(VI)}$$

It has been found (Brunt, 1934, quoting Gold, E.) that the direction of the observed horizontal wind at 500 metres above the ground is almost exactly along the mean sea-level isobars. For the surface wind many forecasters in medium latitudes assume a cross-isobar angle of about 20°, this angle decreasing most rapidly with height near the ground. In this paper we are not concerned with the lowest layers of air, as their temperature will depend largely on that of the surface below them and assumptions of adiabatic lapse rate will be incorrect. It is the air-layers at several hundred feet above the surface that we must deal with, and a cross-isobar angle (associated with friction) of, say, $\theta = 6°$ seems reasonable.

Taking an angle of slope of the air-current with the horizontal of $\beta = 3°$, and putting $\rho = 10^{-3}$ gm./c.c., $v = 10^3$ cm./sec., $l = 7 \times 10^{-5}$, $H = 1$ km. $= 10^5$ cm., we get for the frictional pressure change associated with flow up or down the slope of an escarpment a little over 3000 feet high:

$$\Delta P \text{ (friction)} = \frac{6}{3} \cdot \frac{10^{-3} \times 10^3 \times 7 \times 10^{-5}}{10^3} \times 10^5 = 0{\cdot}014 \text{ mb.}$$

This component is far smaller than either of the other two considered earlier. The very rough nature of the calculation must, however, be remembered. Inclined air-flow is probably more turbulent than the horizontal flow of air of the same lapse rate moving at the same speed. Often, too, the terrain along escarpments is particularly rough and turbulence may be further increased. For these reasons it is likely that the estimate given above is too low. Nevertheless, even if a tenfold increase were admitted, it still appears that the hydrostatic and accelerational terms are the main ones to be considered, with friction to be taken into account as a correction term only.

Upper-Level Pressure Field.

The total pressure difference between B and C in fig. 2 will now be considered. (A is sufficiently far from the slope for vertical velocity and acceleration in column AC to be small.) Clearly the pressure difference between B and C must balance the sum of the components of the pressure summed along BAC, so as to make the pressure single-valued, *i.e.*

$$(P_C - P_B)_{\text{Total}} = \Delta P = \rho_0 H \left[\frac{gH}{T_0} \left(\frac{\Gamma - \Gamma_1}{2} - \frac{\Delta g}{R} \right) + \Delta g \right] \pm \frac{\theta}{\beta} \bar{\rho} \bar{v} l H \text{ dynes/sq. cm.} \quad \text{(VII)}$$

Here θ is the angle which the wind would make with the isobars when flowing horizontally at the same height above the ground and with the same value

(and distribution) of eddy viscosity. The positive sign is to be taken when the flow is up-slope, negative for downwards motion. If the principle of equality of the hydrostatic and the accelerational terms is accepted, then

$$\Delta P = \frac{\rho_0 g H^2}{T_0}(\Gamma - \Gamma_1) \cdot \frac{RT_0}{gH + RT_0} \pm \frac{\theta}{\beta} \cdot \bar{\rho}\bar{v}lH \text{ dynes/sq. cm.,} \qquad \text{(VIII)}$$

or, approximately,

$$\Delta P \approx \frac{H^2}{T_0 \times 10^3}(\Gamma - \Gamma_1) \text{ millibars.} \qquad \text{(IX)}$$

On a chart the pressure difference shows up as follows. Looking along the lines of flow from lower to higher levels (irrespective of whether the air is ascending or descending), one looks across the upper-level isobars (or contour lines) towards lower pressures. This must occur at each level where ascent or descent takes place.

Effect of Turbulence.

If the air becomes very turbulent during its ascent or descent, then the effect of friction on the upper layers will increase, as has already been mentioned. Turbulence will, however, also change the lapse-rates. Streamlines running smoothly up or down the slope no longer exist, and we can only substitute a line of "mean flow", into which air from both upper and lower layers is injected. The fall of temperature along such a line of mean flow will not in general be adiabatic, but will depend upon the intensity and distribution of turbulence and upon the potential temperatures of the neighbouring layers.

If turbulence is not extreme, and if the lapse-rate of potential temperature is roughly linear, then the value of Γ should not be very seriously altered, as the heat gained from the overlying layers of higher potential temperature will approximately balance the heat lost to the lower layers. The lapse-rate along the vertical will, however, be increased by turbulence, and it may be necessary to use a mean value for Γ_1 instead of taking its value at the foot (or summit) of the slope as constant.

Application to Weather Chart.

For air to rise from any given level to the top of an escarpment or mountain range, the upper-level pressure difference can be calculated from equation (IX). If the necessary pressure difference can be found at points on the crest in the general direction of flow and towards the low-pressure side, then it is probable that the ascent will take place. If it is necessary to

go a very long way along the length of the escarpment to find points giving the necessary difference of upper-level pressure, then the slope of the air-current, β, will be much smaller than the gradient of the escarpment, as the air will climb obliquely. The small value of β makes the last term in equations (VII) or (VIII) large, and allowance must be made for friction. The angle θ may perhaps be estimated from the behaviour of the air mass on level ground, and then adjusted by experience to allow for the increased eddy-friction when climbing. If the angle is extremely small, *i.e.* if the air climbs the gradient very obliquely to find the necessary pressure difference, then gain or loss of heat by the moving air may be appreciable and the calculations given above will not apply without modification. As an example, the plateau-level (1200 g.d.m.) pressure difference between Durban and Pretoria has already been mentioned as giving an indication of whether or no sea air will be able to climb the escarpment into the Transvaal. In this case the air climbs obliquely up a long slope and the frictional term is not likely to be negligible.

In all cases of inclined air-flow, whether upwards or downwards, the pressure must increase (throughout the depth of the effect) in the direction from B to C in fig. 2. This effect is illustrated for subsiding air by the South African Coastal low. Here there is a deep anticyclone seawards, with a small depression on or near the coast and at the foot of the escarpment. The air is hot and dry and so pressure falls slowly with height. The pressure gradients are as described above for association with subsidence. At times the subsiding air may not reach the surface, and the hot, dry berg wind is not experienced and can only be detected by upper-air observations.

Acknowledgments.

I wish to thank Professor R. W. James and members of the Departments of Physics and of Mathematics of the University of Cape Town, and also Mr. S. P. Jackson of the University of the Witwatersrand, for valuable criticism.

NOTE.

Since completing this paper, journals containing recent researches by Queney (Queney, 1948) and by Hess and Wagner (Hess and Wagner, 1948) have arrived in this country. Queney's work covers a wide field and is of the greatest interest. It appears, however (not all his papers are available here), that his basic equations (Queney, 1936) postulate frictionless and non-divergent flow over obstacles of infinitesimal vertical height. These limitations are apparently unavoidable because of mathematical difficulties which would otherwise arise. It is, therefore, not clear that his conclusions

can be applied quantitatively to the case treated (in a simpler way) in this paper, viz. the flow of air over an escarpment of finite height, where considerable divergence must occur.

The main purpose of this work is to establish a condition necessary for the air to climb over the escarpment. In many cases the air tends to move round, almost along the contour lines, as pointed out by Queney (Queney, 1936). The common occurrence of orographic rain, of up-slope fogs, of föhn and of berg winds, however, show that in other cases considerable vertical movement takes place. The present paper investigates the pressure gradient necessary for such a flow. No special form of the flow has been assumed, and the resulting equation has a wide validity. The knowledge of the pressure gradient required may be used to forecast whether or no the air will climb the escarpment.

In discussing the magnitude of the acceleration term it has been assumed that at some level above the obstacle the disturbance will vanish. Such nodal surfaces are actually found by Queney (*loc. cit.*), though above the nodal surface a new disturbance (with, roughly, a reversed phase) may appear. Nodal surfaces were found also, for air-flow over the Rocky Mountains, by Hess and Wagner (*loc. cit.*). The discussion given here on the accelerational term is, therefore, not invalidated.

It is of interest to note that in the cross-sections presented by Hess and Wagner (*loc. cit.*) for air-flow over the Rockies the isolines of potential temperature often run nearly horizontally, at least on the western side of the highest range. It seems that in many cases the lower layers of air do not climb over the mountains but form a sort of cushion over which the upper flow takes place.

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MIGRATIONS OF THE CAPE HAKE OR STOCKFISH (*MERLUCCIUS CAPENSIS* CAST.) ON THE WEST COAST OF SOUTH AFRICA.

By E. R. Roux, Botany Department, University of the Witwatersrand.

(With six Text-figures.)

Introduction.

Fish of the genus *Merluccius* form the basis of trawling industries in the four quarters of the Atlantic Ocean. Atlantic forms of the genus are at present divided into four species, viz. *Merluccius merluccius* (= *M. vulgaris*), the European hake, found off the west coast of Britain and as far south as the Cape Verde and eastward into the Mediterranean; *M. capensis*, the Cape hake or stockfish, ranging from Angola to Natal; *M. bilinearis*, the silver hake or "whiting" of the north-west Atlantic; and the Patagonian hake, *M. hubbsi*, found in the south-west Atlantic.

Whether these four divisions represent distinct species or merely a series of overlapping geographical forms has not been finally settled. Some doubt exists as to whether *M. merluccius* and *M. capensis* are in fact separate species (Barnard, 1925). Hart (1946) states that *M. hubbsi* in general body proportions resembles *M. bilinearis*, from which it is nevertheless distinct, and that it is specifically distinct from *M. gayi*, the Chilean hake, found to the west of the Magellan Straits. Whatever the differences between these different forms of hake there is little doubt that their general habits are similar. All are found in comparatively temperate waters, with numbers tailing off towards the tropical and sub-arctic regions. The European hake has been intensively studied by Hickling (1935), and his investigations have provided a useful background for the study of hake in other areas.

The chief points made by Hickling in his description of the migrations of the European hake are as follows: "Each year there is a more or less regular movement of the hake. In summer they invade the shallow waters inside the 100-fathom line and in winter they withdraw again into the deep water." The larger females (forming the bulk of the larger hake—since females grow more rapidly than males) move inshore first. The hake therefore move shoreward in a double wave. This has been shown by Hart to be true also for *M. hubbsi*. There is some evidence, in the case of both

M. merluccius and *M. hubbsi*, that the movements of the larger fish are more rapid and extensive than those of the smaller ones.

The West Ground.

The migrations of the Cape hake described in this paper are derived from the study of catches made over a period of eight years on the West Ground lying west and north-west of Cape Town. Though the surveyed trawling area in this neighbourhood extends over 60 miles north and south and is about 20 miles wide, trawling has been very largely confined to a region of about 10×10 square miles lying roughly 40 miles north-west of Table Bay and having an average depth of 150–175 fathoms. Trawlers have seldom gone beyond 200 fathoms, while trawling to the landward side has been impossible owing to the nature of the sea-bottom. In the absence of data showing catches at different distances from shore, recourse has been had to an intensive study of the fishing on this single spot. The conclusions derived are therefore hypothetical at present, though they appear reasonable when what is known of the migrations of hake in other parts of the Atlantic is taken into account.

Though the West Ground has been regularly fished by Cape Town trawlers since the early 1920's, the records of catches made prior to 1940 are of little scientific value, owing to the practice of discarding unmarketable fish, which prevailed prior to that date. Since 1940, however, the dumping of edible fish has been forbidden by law. Fortunately for the trawling companies the new regulation coincided with a vastly increased demand for fish, a result of economic conditions caused by the war. In recent years, when the supply of small fish again threatens to exceed the demand, an alternative use has been found for them in the manufacture of fish-meal.

Material and Methods.

The data used in this paper are based on records kindly supplied by the firm of Irvin & Johnson (S.A.), Ltd., who have landed over 80 per cent. of the hake trawled from the West Ground. Figures given are derived from trawler declarations of baskets of cleaned (*i.e.* headed and gutted) fish. Hake is usually sorted into the trade categories of "large", "medium", "small", "prime," and "haddocks". The categories have been changed from time to time, but an attempt was made to take these changes into account when compiling the data.

At all times the trawlers have landed a small proportion (8–12 per cent.) of "haddocks" (small hake averaging 1·5 lb., headed but not gutted) and occasionally a number of "round haddocks" (small entire hake). For the purposes of this investigation the following categories were adopted:—

Large: corresponding to trade category "large". Average clean weight 8 lb.

Medium: corresponding to "medium" and "medium-small". Average clean weight 5 lb.

Small: corresponding to "small" and "prime", including also "haddocks" and "round haddocks". Average clean weight 2 lb.

The corresponding average live weights, lengths and ages for these categories are roughly as follows:—

	Live weight in lb.	Length in inches.	Age in years.
Small . .	2½	20	male 5½ female 4½
Medium . .	6½	26	male 7 female 6
Large . .	10½	31	male * female 7

* There are very few males exceeding 25 inches in length.

Lengths were calculated from length-weight graphs, and ages on the assumption of an average growth rate per year of 3¾ inches for males and 4½ inches for females (*cf.* Roux, 1947).

In estimating the density of the hake population on the ground at any point of time, the figure used is the catch per trawler per day. This is obviously less satisfactory than the catch per hour's actual trawling used by many fishery investigators elsewhere; but it has had to serve in view of the absence of more detailed trawling records. No allowance has been made for possible cessation of trawling in bad weather, but in view of the short distance from port at which trawlers operate, and the fact that they almost invariably return in bad weather, it is probable that the error involved is not considerable.

The length of time individual trawlers remained at sea varied considerably. Prior to the war it was usually 3 or 4 days. During the war and subsequently it has generally been 5 or 6 days. But a constant schedule was maintained throughout the eight years, by which landings occurred twice weekly, some boats coming in while others remained at sea. The original figures therefore gave two sets of catch data per week. In this paper the results are stated as monthly averages.

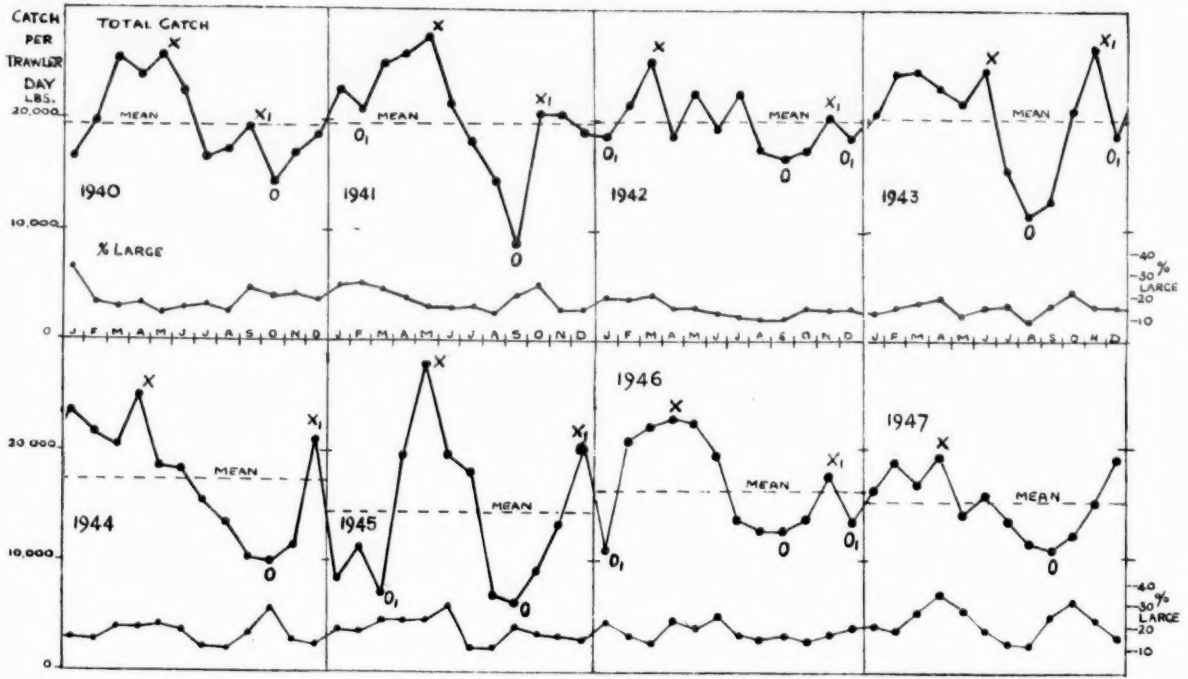

FIG. 1.—Details of monthly catch per trawler/day of total hake, and percentage large in catch, West Ground, 1940–47. Mean annual catch per trawler/day also shown. For symbols (X, X_1, O, O_1) see text.

Analysis of Data.

The data for the eight years covered by this investigation are given in graphical form in figs. 1 to 4. The results are all stated in terms of weights of cleaned fish per trawler per day.

Fig. 1 is a continuous record of the monthly catch per trawler per day for total hake, covering the period January 1940 to December 1947. On the same graph are shown the corresponding percentages of large fish in the catch. The mean annual catches per trawler/day are also given.

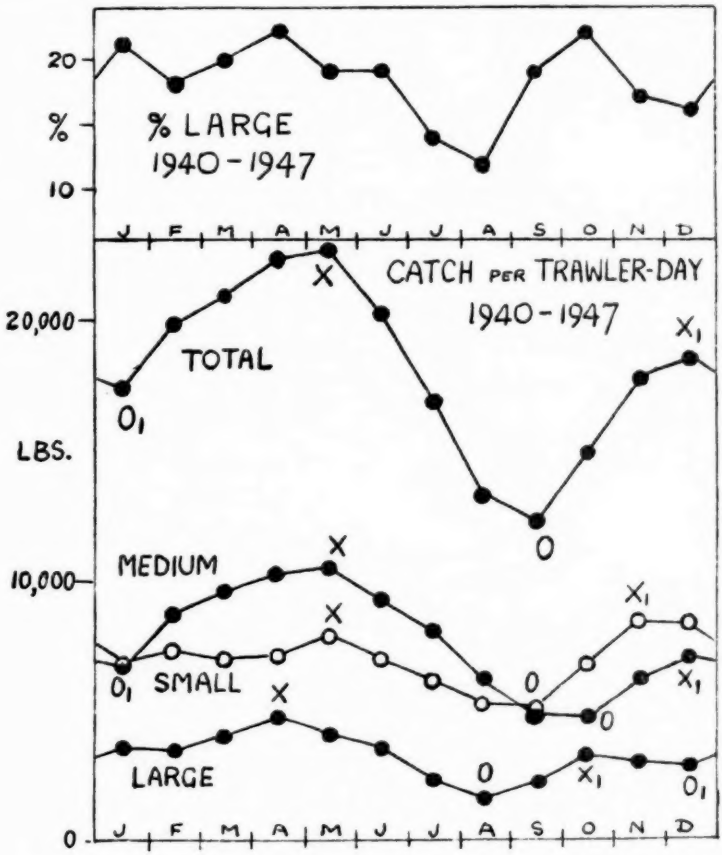

Fig. 2.—Eight-year means of monthly catch per trawler/day for different size groups, and percentage large, West Ground, 1940–47.

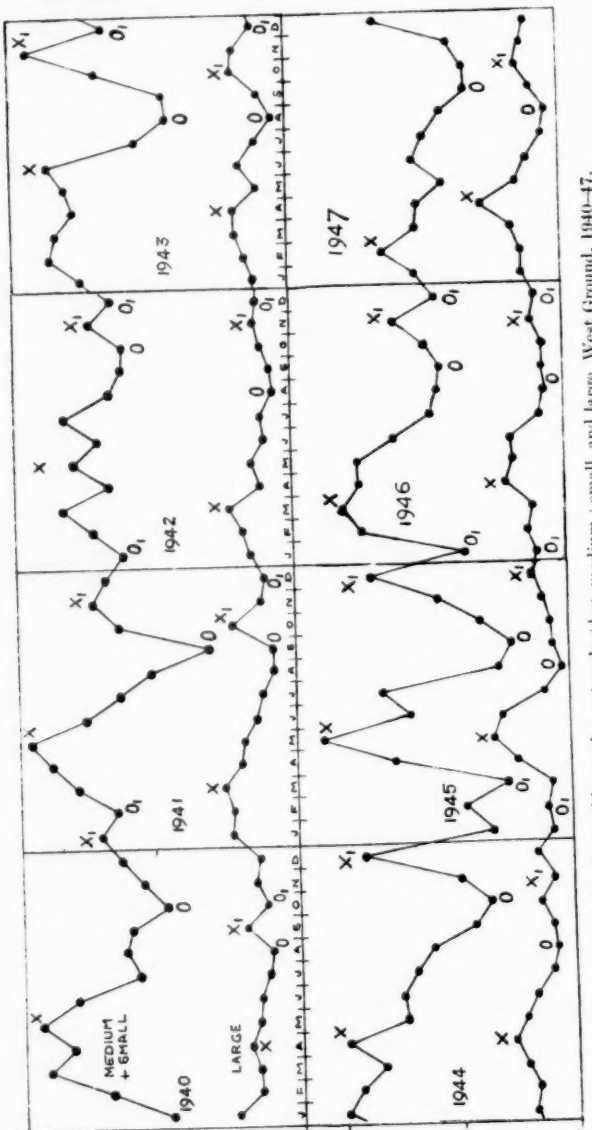

FIG. 3.—Details of monthly catch per trawler/day, medium + small, and large, West Ground, 1940–47.

In fig. 2 are shown the 8-year means of the monthly catches for total, large, medium and small hake, together with the means for percentage large.

Fig. 3 gives details of the monthly catch per trawler per day for (*a*) large hake, and (*b*) medium and small hake together. Eight-year-mean monthly catches per trawler per day for these two categories are shown in fig. 4, together with standard errors. From this graph and fig. 2 the theory of the average annual migratory pattern has been derived.

In all the graphs certain important points in the curves have been indicated by symbols, as follows:—

X = maximum concentration of fish on ground; fish moving offshore.
X_1 = sub-maximum concentration of fish on ground; fish moving inshore.
O = minimum concentration of fish on ground; limit of offshore migration.
O_1 = sub-minimum concentration of fish on ground; limit of inshore migration.

From fig. 1 it is clear that seasonal changes in the catch of total hake have varied considerably from year to year. Fishing is usually at its best in late summer or autumn, at its worst in late winter or early spring. The mean annual catch per trawler/day was almost constant during the four years 1940–43, fell to a low level in 1945 and subsequently rose slightly. Seasonal fluctuations were least in 1942 and greatest in 1945. The latter year contains both the lowest and the highest catches on record. The difference between a good and a bad year seems to be determined mainly by changes in the migratory pattern.*

In addition to the maximal and minimal points mentioned, there are interesting sub-maxima and sub-minima. From the 8-year-mean monthly curves shown in fig. 2 the following generalisations may be made:—

(1) The total catch is on the average at a maximum in May, falls to a minimum in September, rises to a sub-maximum in December, falls to a sub-minimum in January, then rises again till May.

(2) The catch of large hake is usually maximal in April, minimal in August, with a sub-maximum in October and a sub-minimum in December. In other words, the movements of the large hake are, in the average year, consistently in advance of those of the remaining categories. These differences in the behaviour of the large hake are emphasised in the curve showing percentage large. There are two maxima (in April and October respectively), a minimum in August and a sub-minimum in December.

(3) The seasonal curves for medium and small are on the whole similar to the curve for total hake: together these in fact make up the bulk of the

* The question whether the West Ground is being overfished will be the subject of a separate paper.

catch. In the case of small hake the 8-year average catch for November and December actually exceeded the catch for May.

Theory of Migrations.

In formulating a theory of migrations from the facts presented, it is assumed (1) that the major movement of hake is inshore and offshore, as is the case with hake elsewhere, and (2) that the inshore movement is in the spring and summer, the offshore movement in the autumn and winter. The assumptions seem to be justified, firstly because they fit the facts, and secondly because they conform to the well-known movements of hake elsewhere in the Atlantic. The theory may best be explained by reference to fig. 4, which shows the 8-year averages of monthly catches of large hake compared with medium plus small (which together may be conveniently termed "smaller").

One may for convenience regard the hake population of trawlable size as consisting of two enormous major shoals, one comprising large and the other smaller hake. These shoals probably have an indefinite north and south extension along the west coast within the region where the hake is found. To the landward and seaward sides they thin out. Thus each shoal at any moment has an area of maximum fish density, with lower densities to landward and seaward. The two shoals naturally overlap to a large extent and form, in fact, a single shoal of fish of all sizes.

Starting in *August*, we can picture the *large* hake as having reached the limit of their seaward migration. The centre (region of maximum density) of the shoal of *large* hake is now far off in the deep water. The catch of *large* on the ground and also the percentage of *large* in the catch are at a minimum. The majority of the smaller hake are still moving seaward.

In *September* the *large* hake have begun to return to the ground. The density of *smaller* hake on the ground has now reached a minimum, indicating the end of the offshore movement. The percentage of *large* in the catch has risen markedly. The total catch is at a minimum.

In *October* the densest part of the *large* hake shoal is now centred on the ground. There is a sub-maximal peak in the curve for *large*, and their percentage in the total catch is at a maximum. The *smaller* hake have started on their landward migration.

In *December* the *large* hake shoal has reached its farthest inshore limit. The percentage *large* in the catch and the density of *large* on the ground both show sub-minima. The shoal of *smaller* hake is now centred on the ground, having come in from the seaward side. The catch of *smaller* hake now shows a sub-maximum.

In *January*, *large* hake, now moving offshore, have begun to return to

the ground, while the *smaller* hake have reached their farthest landward extension, showing a sub-minimum in the catch.

In *April* the centre of the shoal of *large* hake, on its way seaward, is

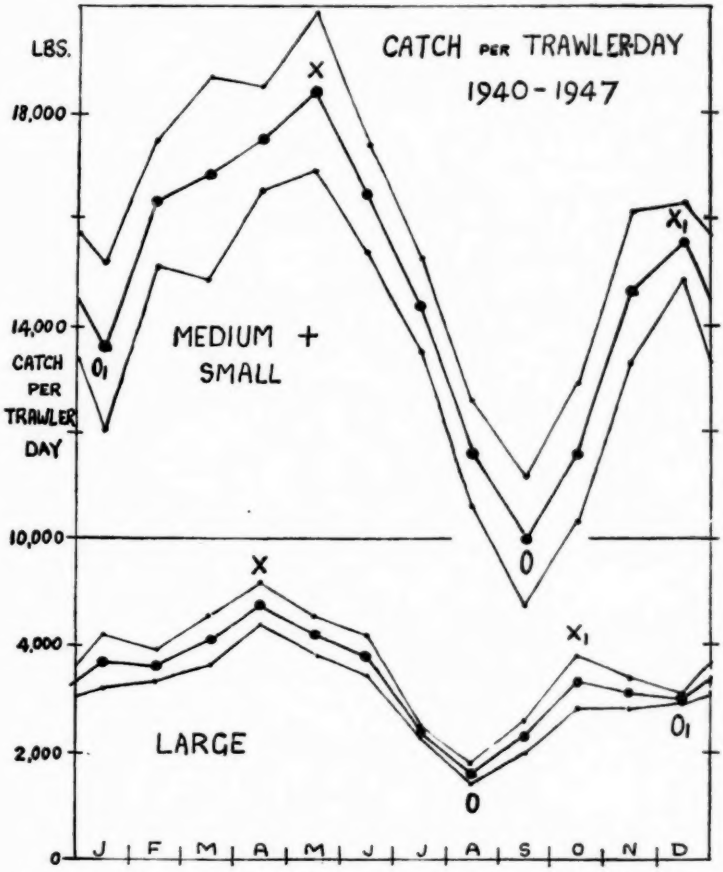

FIG. 4.—Eight-year means of monthly catch per trawler/day, with standard errors, medium + small, and large, West Ground, 1940–47.

passing over the ground. At this time the density of large is at a maximum, and it seems probable that the shoal has now a smaller extension in space, with a correspondingly higher density at its centre than it has at any other time. The centre of the shoal of *smaller* hake, also moving seaward, is close to the ground, though not quite on it.

In *May* the centre of the shoal of *large* hake is just to seaward of the ground, while the shoal of *smaller* hake is centred on it. The catch of *smaller* hake is at a maximum. Also the total catch is maximal.

From now on until August the major movement of all hake is towards the deep water, with declining catches of both *large* and *smaller*.

The above general scheme refers only to the average migratory pattern as observed over eight years. It is quite clear from fig. 3 that there were considerable variations in the pattern from year to year. Thus, while the beginning of the inshore movement of large hake occurred in August, in seven out of the eight years* the centre of the shoal passed over the ground in September of 1940, in October of 1941, 1943, 1944 and 1947, in November of 1942 and 1946, and not until December of 1945. In spite of these variations, however, the inshore movement of *smaller* hake in the spring always began after the inshore movement of the *large* hake, except in 1943, when *large* and *smaller* both showed minimum catches in August. Again, the centre of the shoal of *smaller* hake passed over the ground on its presumed landward migration in November of 1941, 1942, 1943 and 1946, in December of 1944, 1945 and 1947, and not until January in the summer of 1940-41.

The specific differences in migration shown by *large* in relation to *smaller* have been found also to hold good in a general way when *large* and *medium* are compared. It appears therefore that only when the hake reach a weight of over 6 lb. (clean weight, equivalent to a round weight of about 8 lb. and a length of about 28 inches) do they begin to behave on the average in a markedly different manner from the rest of the shoal—as far as one can judge from the seasonal changes in catch on the West Ground.

The great majority of hake of this size (28 in.) and over have been found to be females. Mr. J. M. Rattray (unpublished data) suggests that while sexually mature females of the Cape hake are found from 20 inches upwards in length, it is not till they reach a length of 33 inches that all females are found to be sexually mature. It is possible that a change in migratory habits coincides with the development of sexual maturity. On the other hand, "there is considerable diffuse evidence that the speed and extent of migratory movement is a function of the size of fish" (Hart, 1946).

Supplementary Evidence from the North and East Grounds.

The theory of migrations described above does not particularise as to the extent of the movements of hake of different sizes beyond the limits of the West Ground. In the case of European and Patagonian hake there is strong evidence that during the offshore migration the larger fish move farther out

* The exceptional year was 1941, when the catches of *large* in August and September were equal.

to sea than the smaller ones. This may very well be so in the case of *M. capensis* off Cape Town, though direct evidence is lacking. With regard to the extent of the inshore migration, catch data from the two other hake trawling grounds off the South African coast may be of interest. The East Ground * is a large area extending roughly between Port Elizabeth and Mossel Bay on the south-east coast, where trawling is usually done at about 50 fathoms. Average annual sea temperatures here are considerably higher than off Cape Town (*cf.* Roux and Molteno, 1946). No detailed study of catch data from this region has been made, but Cape Town trawlers operating there never land any hake except "medium". Possibly small quantities of "large" and "small" fish are caught, but their number does not warrant their sorting into separate baskets.

The North Ground lies between Port Nolloth and the Orange River mouth, where trawling is done in 40–50 fathoms. Trawlers began to visit it regularly in February 1945. Average sea-surface temperatures there are almost certainly lower than off Cape Town (Marchand, 1930). Catch data from this ground have been systematically collected since regular trawling began. Monthly averages of catch per trawler per day are shown in fig. 5. The density of the hake population during the three years on this new ground was extremely low, average maxima there being lower than the average minima on the West Ground. Maxima appeared to be somewhat earlier (February–March) and minima somewhat later (November) than on the West Ground, but in view of the brevity of the record these differences may not be significant. During 1945 trawlers sorted "large" from "medium", but this practice was discontinued in subsequent years. An interesting fact about this North Ground is the almost complete absence of small hake and the comparative absence of large hake for most of the year.† The difference in size-composition of catches from the North and West Grounds is brought out clearly in the length-distribution curves shown in fig. 6. These are smoothed curves made from length measurements of typical hauls of hake from the two grounds. In the case of the West Ground there is always a definite "mesh-selection" peak at 19 inches. Fish of this length and over are unable to escape once they are in the cod-end of the trawl with its regulation 2-inch-bar mesh. Fish less than 19 inches may escape, their chances of doing so being roughly inversely proportional to their size. This mesh-selection peak has never occurred in length-distribution curves of

* This was the first ground to be exploited by the South African hake-trawling industry.

† The comparative absence of large hake on the North Ground cannot be due to a difference in growth rate. Estimated growth rates of male and female hake caught on this ground do not differ significantly from those of hake taken on the West Ground.

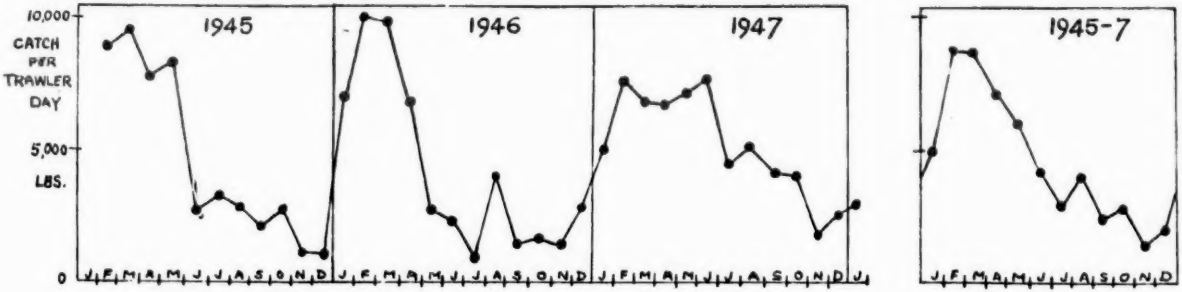

FIG. 5.—Details of monthly catch per trawler/day of total hake, North Ground, 1945–47. Also three-year monthly means.

hake caught on the North Ground, indicating an almost complete absence of fish less than 20 inches long.

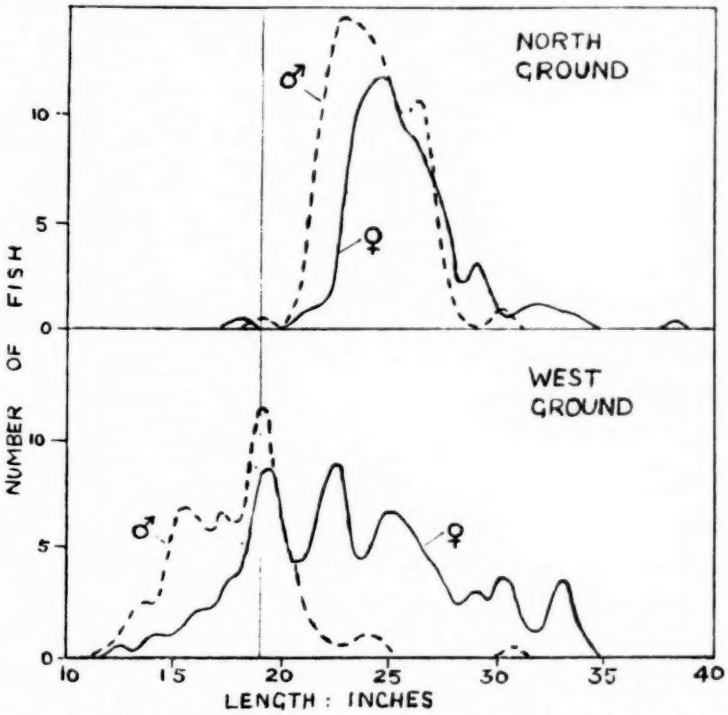

Fig. 6.—Typical length-distribution curves (smoothed) of hake, trawled on North and West grounds.

Discussion.

The fact that two shallow-water regions so different in latitude and sea-temperature as the North and East Grounds show hake populations consisting almost exclusively of medium-sized fish throughout the year, suggests that we may be concerned with a general feature in the migrations of *M. capensis*; though we have no direct evidence that medium hake off Cape Town actually move farther inshore than either large or small hake.

That small hake have a more restricted range of movement than medium and medium than large may be assumed with a fair degree of confidence, not only from general principles, but from the fact that the range of seasonal

variation in the catch of these three classes on the West Ground is strictly related to their size (see fig. 2 and Table I).

TABLE I.

	8-years average monthly catch per trawler/day (lb.).		Minimum as percentage of maximum.
	Maximum.	Minimum.	
Large . . .	4,800	1,600	33
Medium . . .	10,500	4,800	46
Small . . .	7,900	5,100	65
Total hake . .	22,600	12,300	55

Tentatively the following scheme is suggested for the range of migrations of *M. capensis*. Small hake have a limited range of movement in waters of intermediate depth. Medium hake have a wider range, both inshore and offshore. Large hake may have the widest range of all, but do not appear to come as far inshore as do medium hake.

SUMMARY.

1. The relations of the Cape hake or stockfish (*Merluccius capensis*) to other forms of hake found in the Atlantic are briefly discussed.

2. Data covering the catch of Cape hake during eight years on the trawling area (West Ground) lying west and north-west of Table Bay are analysed, and a provisional hypothesis regarding the migrations of this fish is put forward. In most particulars the hypothesis conforms with what is known of hake migrations in other parts of the Atlantic.

3. The West Ground is so situated that trawling does not occur either on the landward or seaward sides. Consequently a theory of migrations must be based on fluctuations in the density of the hake population on the ground itself, where depths are between 150 and 200 fathoms.

4. Hake caught in the trawl are classified as large, medium and small, while the density of fish on the ground at any time is expressed as weight of catch per trawler per day's fishing.

5. The hake population as a whole moves inshore in the spring and summer, offshore in the autumn and winter.

6. Large hake (consisting mainly of females) appear to move more

rapidly than the other categories, their movements to or away from the ground normally preceding those of the others. The numbers of large hake on the ground show a maximum, medium hake an intermediate, and small hake a minimum degree of fluctuation.

7. Evidence obtained from the North Ground (in the Atlantic between Port Nolloth and the mouth of the Orange River) and the East Ground (in the Indian Ocean between Port Elizabeth and Mossel Bay) shows that in shallow waters (40–50 fathoms) small hake are never found, while large hake are extremely rare. It seems probable therefore as a general rule for *M. capensis* that medium fish move farther inshore than either large or small fish.

8. Good and bad fishing years on the West Ground are probably due mainly to variations in the speed and duration of inshore and outshore movements of the shoals.

ACKNOWLEDGMENTS.

Thanks are due to the firm of Irvin & Johnson (S.A.), Ltd., who allowed the writer access to their fishing records, and to Professor J. H. O. Day of the University of Cape Town for useful criticism and advice.

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A NEW DIATOM FROM SOUTH AFRICA—*CHAETOCEROS PARALLELIS*.*

By B. P. Boden,

Scripps Institution of Oceanography, La Jolla, Cal.

(Communicated by J. H. Day.)

(With one Text-figure.)

(Read November 19, 1947.)

(Latin Summary of the Species available if required.)

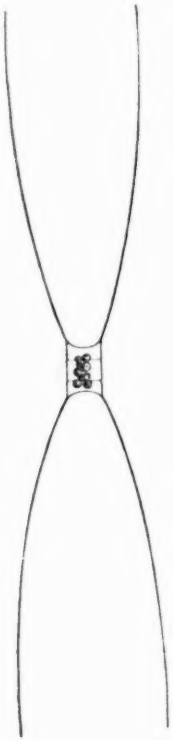
Chaetoceros parallelis n. sp.—Cells solitary, rectangular in broad girdle view. Valves concave, elliptical in valve view. Valve mantle fairly high, with slight constriction at junction of valve mantle and girdle zone. Slender setae originate at cell corners and run almost parallel with pervalvar axis, slightly convex on outside. Chromatophores numerous cocciform bodies. Width of cell in girdle view 10·8–13·5 μ, length 21·6–28 μ, length of setae 121–135 μ.

This delicate form occurred in collections made in the neritic province of the west coast of South Africa between Lamberts Bay and Cape Point.

It is tentatively placed in the section Simplicia although its numerous chromatophores may exclude it from this section.

* Contributions from the Scripps Institution of Oceanography, New Series, No. 449

[*See overleaf for fig.*



THE RELATIONS OF THE CAPE AND THE KARROO FLORAS NEAR LADISMITH, CAPE.

By Margaret R. Levyns.

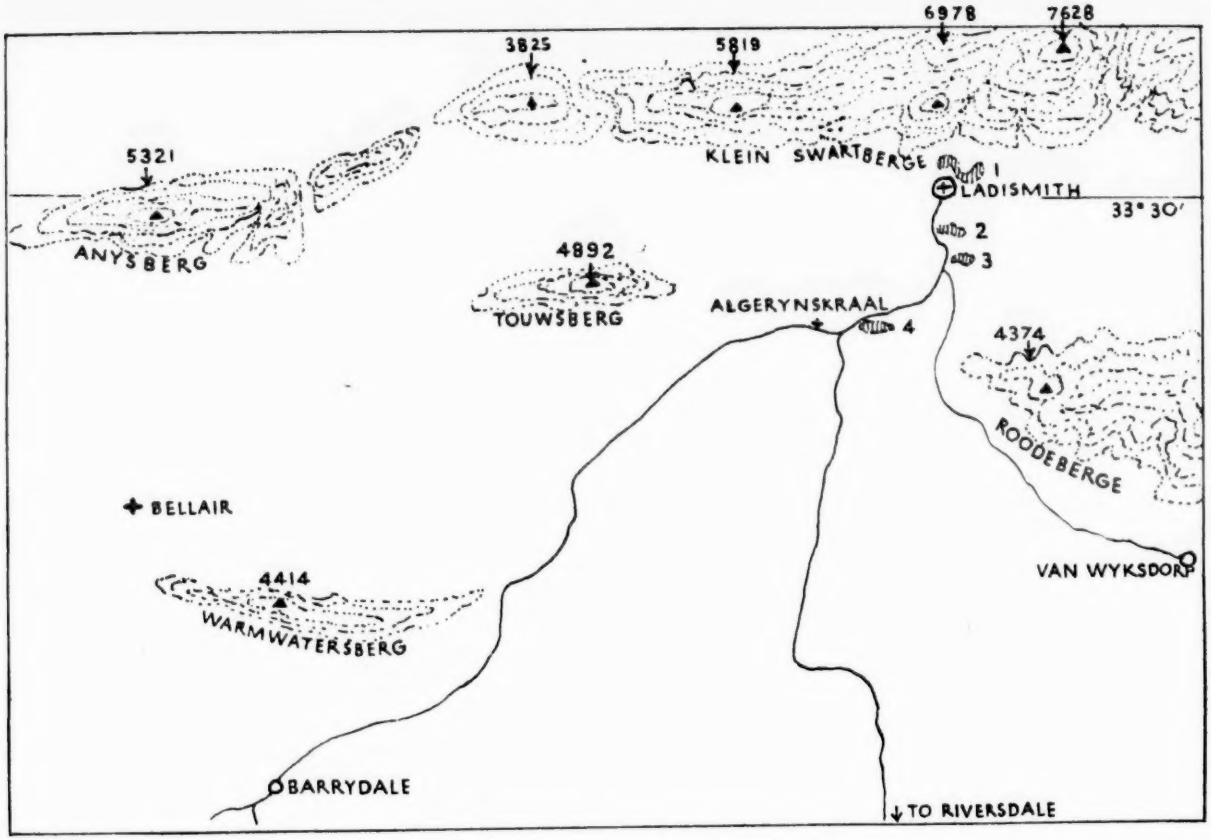
(With Map and ten Text-figures.)

(Read November 17, 1948.)

The Cape flora is generally acknowledged to be extremely old, possibly the oldest of the floras which occupy the continent of Africa at the present time. It has always excited the interest of botanists, and yet its origin remains a profound mystery. We know little of the geographical distribution of the majority of its constituent elements, and combined geographical and taxonomic studies may well provide valuable clues as to its origin. Another line of research which may give useful information is a study of the behaviour of the Cape flora in regions where it comes in contact with the other African floras. In the eastern parts of the Union, where several distinct floras mingle, the problem is very complicated. In those parts of the western districts, however, where the Cape flora meets the succulent bush of the karroo, the relations are relatively simple. There are only two floras, and it is possible to obtain information as to the conditions under which each particular assemblage of plants may exist. The following account deals with the relations of these two floras in the neighbourhood of Ladismith.

A mile or so to the north of the town the mountain range, rather inaptly termed the Klein Swartberge, rises to heights in the neighbourhood of seven thousand feet. These mountains have a great effect upon the rainfall, so that on the mountains themselves the precipitation is considerable, while only a few miles to the south in the Little Karroo arid conditions are found. It is the grading in rainfall which makes this region exceptionally interesting to the plant geographer.

This paper does not deal with the vegetation of the Klein Swartberge, but with that of a series of kopjes, all under a thousand feet high. Consequently their altitude will be insufficient to have any effect upon the rainfall and thus upon their vegetation. These kopjes are shown on the accompanying map. Kopje 1 lies between the foot of the main mountain



Map of the Ladismith district. The altitude of the main mountain peaks is given in feet. The main roads to the south of Ladismith are shown.

range and the town of Ladismith. As it lies nearer the mountain its rainfall may be a little higher than that recorded for the town. It certainly will not be any less. Kopje 2 lies about 2 miles south of the town on the eastern side of the road to Barrydale. Kopje 3 is similarly situated 2 miles farther on. Kopje 4 is about 9 miles from Ladismith and about 2 miles away from Algerynskraal, for which figures of rainfall are available. The main axis of all the kopjes runs roughly from east to west—an important feature, for the northern slope obtains the maximum amount of sunshine while the southern slope is relatively sheltered. It will be seen later that aspect plays a very important part in determining the type of plant community clothing the slopes.

Geology.

The higher mountains are composed of rocks belonging to the Table Mountain Series, whereas most of the karroo itself is composed of softer rocks belonging to the Bokkeveld Series. However, in the neighbourhood of Ladismith, rocks of Witteberg age are faulted down against the Table Mountain sandstone. Kopjes 1 and 2, and possibly also 3, are composed of Witteberg rocks. The rock fragments strewn over the slopes of all these kopjes contain abundant impressions of Spirophyton, a fossil at one time regarded as a clear indication of Witteberg age. It is now known that Spirophyton may also be found in rocks of the Upper Bokkeveld (du Toit, 1), so its presence on Kopje 3 does not in itself provide proof that the rocks are of Witteberg age. The rocks of Kopje 4 are different from those of the first three, and Spirophyton is absent. There is no doubt that these rocks belong to the Bokkeveld Series. The lithological characters of the four kopjes appear to be somewhat similar, and it is improbable that the features of the vegetation about to be described are due to differences of the soil.

Meteorology.

Rainfall appears to be one of the important factors determining which flora will be found in any particular locality. Higher precipitation favours the Cape flora, which cannot exist below a certain amount. The karroo succulents, on the other hand, are harmed by too frequent rains. It is therefore important to examine closely such rainfall records as exist for this particular area.

Rainfall records (2) have been kept for three stations shown on the accompanying map. The town of Ladismith has an altitude of 1860 feet. Algerynskraal (altitude 1410 feet) is a small settlement on the Barrydale road, and about 2 miles farther away from Ladismith than Kopje 4. Its

RAINFALL STATIONS.
KOPJE.
Map of the Ladismith district. The altitude of the main mountain peaks is given in feet. The main roads to the south of Ladismith are shown.

rainfall may therefore be assumed to be not very different from that of the kopje. The third station, Bellair (altitude 1650 feet), is still farther out in the karroo, and has been included to demonstrate that the rainfall diminishes as the distance from the Klein Swartberge increases. The charts shown in fig. 1 have been compiled from the Government Meteorological Reports for the years 1929–1941. The records are complete for Ladismith, but there are gaps in 1937 for Algerynskraal, and in 1931 and 1932 for Bellair. Years for which records are incomplete have not been taken into account in constructing the diagrams. In row A records are shown for the wettest year during the period in the three stations. Row B shows the records for the driest year. Row C gives the average rainfall for each month taken over the whole period, and indicates clearly that this area lies between the winter and summer rainfall areas and may receive its rain at any time of the year. Row D shows the actual rainfall for each month in the year which approximated most closely to the average annual rainfall for the period. The differences between the diagrams in this row and those in row C bring out clearly the erratic nature of the rainfall. This is an important factor in relation to vegetation, for only plants that are able to survive periodic droughts can exist in places such as this.

The following table summarises a few of the significant differences between the stations:

	Ladismith.	Algerynskraal.	Bellair.
	For a period of 13 years.	For a period of 12 years.	For a period of 11 years.
Annual average rainfall in inches . . .	12·39	6·10	4·54
Number of rainy days per year . . .	from 35 to 49	from 9 to 24	from 7 to 21
Rainless months (Apr.–Sept.) . . .	3	16	20
Rainless months (Oct.–Mar.) . . .	8	23	27

An interesting feature is the marked difference in rainfall in places not far distant geographically. A heavy rainfall in one place is no clue to the precipitation at either of the other stations at the same time.

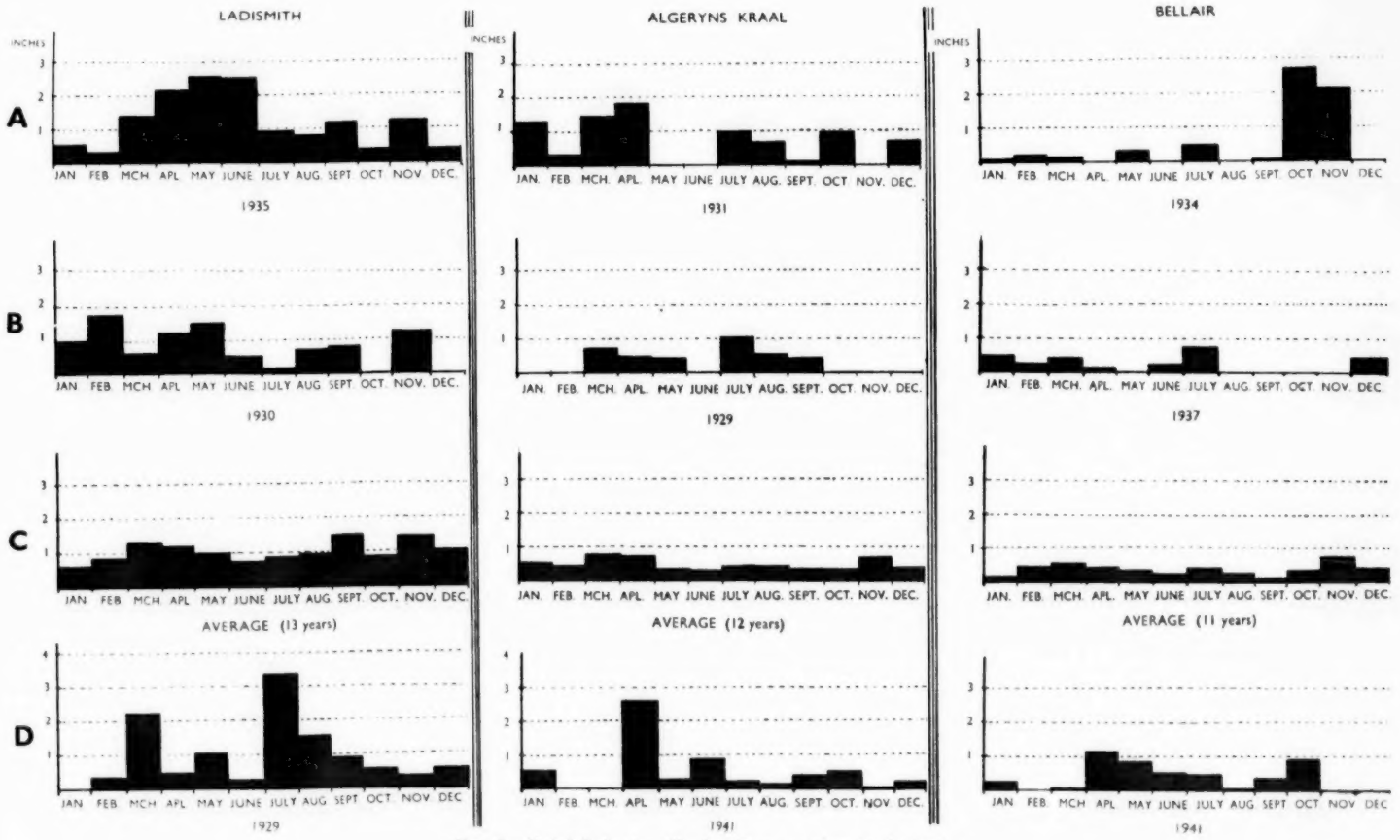


FIG. 1.—Rainfall charts. Explanations are given in the text.

The paucity of rainfall records in the karroo makes it impossible to give accurate data with regard to the four kopjes the vegetation of which is about to be described, but it can be assumed with reasonable probability that the rainfall figures will form a descending series. The data given in fig. 1 and the table show clearly that the amount of rain and its regularity of distribution decrease with the distance from the Klein Swartberge. Thus the kopje with the most favourable climatic conditions is No. 1 and the least favourable No. 4.

A most important factor affecting vegetation is the rate of evaporation, a subject about which information is lacking. It is a matter of common knowledge that the evaporation rate must be high, especially during the summer months, and it is significant that most of the rainless months occur at that time. The northern slopes receive more direct sunlight than the southern. In consequence the soil temperatures are probably higher on the northern slopes, and as a result of this the evaporation rate will be higher. It is extremely unlikely that there is any appreciable difference in rainfall on any given kopje, as they are all low and not very extensive. Yet on the first three kopjes there are striking differences between the vegetation on the northern and southern slopes. These can only be explained by the effectiveness of the rainfall as determined by the rate of evaporation.

Types of Vegetation.

Three easily recognised plant communities are to be found on the kopjes. The term Cape sclerophyll is used here for the first type, which is characterised by fairly large bushes with leathery or ericoid leaves. The presence of the families Proteaceae, Restionaceae, Ericaceae, etc., enable us to identify this type of vegetation easily. It is the type which constitutes the so-called Cape flora of the coastal strip of the south-western Cape Province. The second plant community, termed rhenosterveld, is almost certainly a development of the Cape sclerophyll, but it so obviously constitutes a distinct unit of vegetation that it is advisable to keep it apart from the true Cape sclerophyll. Low grey-green bushes of *Elytropappus rhinocerotis* (the rhenoster bush) dominate this type of vegetation. The families typical of the true Cape sclerophyll are present either in very reduced numbers or are absent altogether. Succulents are few and play a minor rôle in rhenosterveld. The third type, succulent bush, has large numbers of plants with fleshy leaves or stems. Scattered here and there are a few large bushes with leathery leaves, while much less conspicuous are many small, non-succulent undershrubs. These latter provide most of the good fodder plants of the Little Karroo.

Kopje 1.

The southern slopes of the Klein Swartberge are covered with Cape sclerophyll. The kopje is separated from the mountain by a valley through which a road runs to the fertile little settlement of Hoeko, and it is not more than a mile away from the main mountain mass. The northern slope, however, is not covered with typical Cape sclerophyll, but with rhenosterveld of the type common in the Riversdale area, with *Aloe ferox* as a prominent constituent (fig. 2). As is usual with rhenosterveld, other plants occur amongst the dominating plants of *Elytropappus rhinocerotis*. The principal subsidiary shrubs are *Passerina obtusifolia*, *Dodonaea thunbergiana*, *Phylica purpurea* and *Aster Bodkinii*. On reaching the rocky ridge which crowns the summit of the kopje there is an abrupt change in the vegetation. The rhenoster bush disappears completely, and on descending the southern slope we find ourselves in typical Cape sclerophyll (fig. 3). This is of a highly developed type, with members of Proteaceae, Ericaceae, Restionaceae, Rutaceae and other Cape families conspicuous. Among the Proteaceae, which as usual in this type of vegetation are very conspicuous, we find *Protea macrophylla*, *Protea grandiflora*, *Protea mellifera*, *Leucospermum puberum*, *Leucadendron adscendens*, and an undescribed species of Paranomus. On the upper slopes of the kopje a casual observer might well imagine himself many miles away from the karroo in some part of the Western Province much more favoured climatically than this region. Many characteristic Swartberge plants are found, such as *Metalasia Galpinii*, *Relhania speciosa*, *Polygala pinifolia*, *Passerina obtusifolia*, *Cannomois Dregei*, etc. The Cape sclerophyll persists right to the foot of the kopje, but on the lower part of the slope odd plants of the rhenoster bush will be seen. These increase in frequency until on the level ground rhenosterveld replaces sclerophyll. On this side of the kopje *Aloe ferox* does not form a constituent element of rhenosterveld as on the northern slopes. The subsidiary bushes too are different. Here we find *Aspalathus microdon*, *Polygala teretifolia*, *Chrysocoma tenuifolia*, *Relhania squarrosa*, and one or two shrubby species of Mesembryanthemum. Scattered here and there amongst the rhenoster bushes are a few large shrubs which take the place of *Aloe ferox* on the other side of the kopje. The principal shrubs are *Carissa ferox*, *Gymnosporia integrifolia*, *Rhus undulata*, and here and there a plant of *Dodonaea thunbergiana*.

Kopje 2.

This kopje lies barely three miles to the south of the kopje just described, but its vegetation is entirely different. On the northern slopes in place of

rhenosterveld we find a characteristic succulent bush. *Portulacaria afra* is a prominent member of this community. Other shrubby succulents are *Crassula perfossa, Crassula portulacea, Salsola aphylla, Euphorbia mauritanica*, etc. Scattered about on this slope are some large non-succulent bushes of which *Pappea capensis* is the most common. Others are *Euclea undulata, Gymnosporia integrifolia* and *Rhus undulata* (fig. 4). The vegetation in general is of an open type with small undershrubs scattered among the larger succulent bushes (fig. 5). The smaller non-succulent plants suffer seriously from over-grazing and in most cases are unable to produce flowers. Fig. 6 shows a fairly luxuriant specimen of *Monechma robustum*, a common fodder plant of this part of the karroo. The only leaves which this plant is able to retain are those lying behind the protective entanglement of old, hardened stems. Flowers are scarcely ever seen. This plant and *Pentzia incana* are much sought after by sheep and goats, and the fact that plants manage to survive at all is a matter for surprise. There are several small plants armed with spines which keep most human beings at bay, but which apparently do not act as a deterrent to marauding herbivora. They too are seldom allowed to flower. Amongst these may be mentioned *Dicoma spinosa, Blepharis capensis* and *Pachypodium bispinosum*. Near the top of the northern slope a few plants not seen below begin to appear. They are, in order of appearance, *Polygala teretifolia, Pteronia fasciculata, Nymania capensis* (another plant much favoured by sheep and goats), *Polygala pinifolia, Elytropappus rhinocerotis, Dodonaea thunbergiana, Relhania squarrosa* and *Restio Gaudichaudianus*. They are not abundant, but occur here and there, heralding the change which takes place immediately the top of the ridge is reached.

The sheltered positions afforded by the outcrop of rocks along the top of the ridge lead to the appearance of Cape sclerophyll and the disappearance of succulent bush (fig. 7). The sclerophyll does not approach in luxuriance the same type of plant community on the first kopje, but there is no doubt at all as to its nature. Only two members of the Proteaceae occur, *Protea macrophylla* and *Leucadendron adscendens*. Restionaceae is fairly well represented by *Cannomois Dregei, Thamnochortus fruticosus* and *Restio Gaudichaudianus*. Other characteristic plants are *Metalasia Galpinii, Polygala pinifolia, Aster Bodkinii, Athanasia incisa, Erica Plukeneti*, just to mention a few of the more obvious constituents. At the summit, close to the beacon, are a few plants of *Passerina obtusifolia*, a characteristic plant of the sclerophyll on the first kopje, but much less evident here. Plants of *Elytropappus rhinocerotis* occur here and there in the sclerophyll.

On the southern slopes soon after leaving the summit typical sclerophyll peters out and is replaced by rhenosterveld (fig. 8). It is a drier type of

FIG. 2.—Northern slope of Kopje 1 showing typical rhenosterveld.

FIG. 3.—Cape sclerophyll on the southern slopes of Kopje 1. *Protea macrophylla* is conspicuous in the foreground.

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FIG. 4.—Succulent bush. The photograph was taken on Kopje 3. The shrub in the immediate foreground is a species of Mesembryanthemum. The lighter plants in the middle distance are *Crassula portulacea*. The large shrubs are *Euclea undulata*.

FIG. 5.—A more open type of succulent bush than that shown in fig. 4.

FIG. 6.—*Monechma robustum*, much eaten by sheep and goats.

FIG. 7.—Cape sclerophyll on the top of Kopje 2. Here as in Kopje 1 *Protea macrophylla* is conspicuous.

FIG. 8.—A view taken from Kopje 2 of a similar kopje on the other side of the main road to Barrydale. It shows the difference between the two sides of the kopje. The open type of vegetation (succulent bush) is in marked contrast to the uniform covering afforded by rhenosterveld on the southern slope. The photograph was taken in July and much of the southern slope is in shade.

FIG. 9.—A very old plant of *Portulacaria afra* on the top of Kopje 4.

FIG. 10.—*Pappea capensis* on the top of Koppje 4. The large plant to the left is *Portulacaria afra*.

rhenosterveld than that seen on the northern slopes of Kopje 1, and *Aloe ferox* is completely absent. Growing with the rhenoster bushes are plants of *Aster Bodkinii*, *Chrysocoma tenuifolia*, *Aspalathus microdon*, etc. In a sheltered dry water channel a few plants of *Cliffortia micrantha* were encountered. Until recently this species has been known from two localities only, one on the Anysberg and the other on the Touwsberg. It flowers freely on the mountains during July and August, even under conditions of drought such as have occurred during the winter of this year (1948). On this kopje and on Kopje 3, where it was also found, it bore no signs of flowers. This suggests that the drier conditions of the kopjes inhibit reproduction. If this be so, then this species has reached its limit of tolerance and is in danger of disappearing.

Kopje 3.

The northern slopes are very similar to those of Kopje 2, and most of the plants found there belonging to the succulent bush community are also found here. The only difference noted is that the plants heralding the approach of another type of plant community make their appearance quite close to the summit, and not about a third of the way down as on Kopje 2. The indicator plants were for the most part the same as before, viz. *Pteronia fasciculata*, *Nymania capensis*, *Polygala pinifolia*, *Elytropappus rhinocerotis* and *Dodonaea thunbergiana*.

The top of this kopje, though it has a few plants the same as those in the sclerophyll on the ridge of Kopje 2, has not a plant covering that can be assigned to the Cape sclerophyll. The abundance of the rhenoster bush indicates that it is best classified as rhenosterveld, though it has certain elements which separate it from typical rhenosterveld such as occurs farther down on the southern slope. Large bushes 8 to 12 feet high are scattered about. These are *Rhus undulata*, *Euclea undulata*, *Dodonaea thunbergiana* and *Portulacaria afra*. All but *Dodonaea thunbergiana* are characteristic plants of the northern slopes of the drier kopjes. Smaller bushes are *Elytropappus rhinocerotis*, *Polygala pinifolia*, *Pteronia fasciculata*, *Pteronia incana*, *Chrysocoma tenuifolia*, and a few shrubby species of Mesembryanthemum. In rock crevices plants of *Restio Gaudichaudianus* occur, but this is the sole relic of a family which may be regarded as typical of the Cape sclerophyll.

The rhenosterveld which occupies most of the southern slope agrees very closely with that described for the same slope on Kopje 2.

Kopje 4.

The northern slopes have a drier type of succulent bush than that shown on the two previous kopjes, but the constituent plants are much the same. The plants are more widely spaced and tend to be somewhat stunted. On the previous kopjes *Portulacaria afra* stands erect, and sometimes the plants are almost tree-like in form. Here they lie close to the soil or spread over rocky outcrops.

The top of this kopje is covered with succulent bush, and the vegetation is very similar to that on the northern slopes of Kopjes 2 and 3. *Portulacaria afra* no longer sprawls over the ground as it did on the slope, but has the habit of a small tree (fig. 9). *Pappea capensis* and *Euclea undulata* also become tree-like (fig. 10). Once again the more favourable conditions for plant life on the top of the kopje are reflected in the vegetation, but here, instead of a complete change in the type of plant community, we find one very similar to that on the slope developing more luxuriantly. Various shrubby species of Mesembryanthemum which are rare on the northern slope are common on the top. In addition to the succulents which characterise the top there are three non-succulent species of great interest. *Polygala pinifolia* is fairly common. This is normally a constituent of the Cape sclerophyll, but here it appears out of its element, the sole survivor of a type of vegetation which apparently can no longer hold its own under the arid conditions of the kopje. The ability of this species to resist drought must be the reason for its existence in an alien plant community. *Elytropappus rhinocerotis* is represented by an odd plant or two, but nowhere on this kopje is there any sign of rhenosterveld. There are a few depauperated plants of *Nymania capensis*, much ravaged by goats and looking as if they are waging a losing battle in the struggle for existence. The southern slopes are very similar to the top, though rather less luxuriant. Summing up the features of this kopje, we see that it is clothed with succulent bush throughout but with relics of other communities on the top.

Discussion.

The evidence provided by the rainfall figures for Ladismith and the surrounding parts of the Little Karroo make it reasonable to assume that the four kopjes differ in their rainfall. Kopje 1 has the highest rainfall, but this diminishes as the distance from the Klein Swartberge increases. The kopjes are only a few hundred feet high and not very extensive, so we may also assume that the precipitation on all parts of any one kopje is uniform. However, though the rainfall may be uniform, the evaporation rate is undoubtedly different on the northern and southern slopes. Thus

the amount of water available to the roots of plants will differ with the aspect, the crests and southern slopes always having a better water supply than the northern slopes.

The plant communities on the kopjes are of three kinds, Cape sclerophyll, rhenosterveld and succulent bush. The relationship of these three communities with regard to the available moisture in the soil is clearly brought out on these kopjes. The Cape sclerophyll requires more moisture than the other two, and thus we find it well developed on the southern slope of Kopje 1, which has an average annual rainfall of over twelve inches. It just manages to survive on the crest of Kopje 2 but is not seen on Kopjes 3 and 4. When conditions become too dry for Cape sclerophyll, rhenosterveld takes its place, as is clearly seen on the first three kopjes. On Kopje 1 with its relatively high rainfall it occupies the exposed northern slope, while on the drier Kopjes 2 and 3 it is on the protected southern slopes. On both these latter kopjes succulent bush covers the northern slopes. Kopje 4 with increased dryness cannot support either of the more mesophytic plant communities, and is covered everywhere with succulent bush.

Attention has been focused of late on the karroo and its reported aggressive habits when it comes into competition with grassland. It is therefore pertinent to inquire here whether there is any indication in the Little Karroo of similar aggressive tendencies on the part of the succulent bush community when it comes in contact with the Cape flora. The answer is clearly no. Soil moisture, which is largely based on rainfall, appears to be the primary factor determining the type of vegetation. Here, according to the amount of moisture available, the three communities live side by side, each occupying the niche to which it is adapted. None shows any obvious signs of attempting to encroach on the territory belonging to the others.

Signs of aggression on the part of the karroo flora are lacking. On the other hand there are clear indications of deterioration in that flora due to extensive over-grazing. The valuable fodder bushes of the Little Karroo, of which *Pentzia incana* and *Monechma robustum* are outstanding examples, are slowly but surely being exterminated by the flocks of sheep and goats which eat down these favoured plants till it is difficult to find a well-developed, undamaged leaf. Flowers are rarely seen, and unless some measures are taken these valuable plants are doomed. Under present conditions the deterioration of the veld is progressive. Flocks move indiscriminately over the veld, eating down the favoured shrubs and leaving those which they like less, though many of them are edible. The most satisfactory method of veld management would be to fence in areas, which would then be grazed in rotation. From time to time, especially after a season of good rains, animals should be completely excluded from

certain areas, which would then be able to regenerate. Naturally a scheme of this kind would be expensive. As a temporary expedient, small fenced-in areas to which no animals had access would give plants a chance to regenerate and set seed. Sanctuaries of this kind would help to retain valuable constituents of the karroo flora which under present conditions are unlikely to survive.

Summary.

1. All four kopjes have their long axis running approximately from east to west. They are only a few hundred feet high. The rainfall varies from kopje to kopje, the first having the highest and the last the lowest. The northern slope of each is drier than the southern.

2. Kopje 1 has rhenosterveld on the northern slope; Cape sclerophyll covers the summit and southern slope.

3. Kopje 2 has succulent bush on the northern slope, Cape sclerophyll on the top and rhenosterveld on the southern slope.

4. Kopje 3 has succulent bush on the northern slope, and rhenosterveld on the top and southern slope.

5. Kopje 4 is covered with succulent bush throughout, but with more luxuriant growth on the summit and the southern slope. There are relics of the other vegetation types.

6. There are no signs of aggressiveness on the part of the karroo flora.

7. There are clear indications of the harmful effects of over-grazing on the succulent bush community.

Acknowledgment.

The author wishes to acknowledge her indebtedness to the Council of Scientific and Industrial Research. The observations recorded in this paper were made while holding a Senior Bursary.

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THE PLANT *TEPHROSIA VOGELII*, HOOKER, AS A FRESHWATER FISH POISON.

By K. L. J. Blommaert, M.Sc.,
Inland Fisheries Department, Stellenbosch.

(With two Text-figures.)

(Read November 1948.)

Introduction.

The partial or entire removal of a fish population from a water is sometimes necessary. Some waters are overstocked, whereas others contain inferior or undesirable species. Their elimination is desirable in order to permit restocking, or as a means to the control of infectious disease.

The early introduction in South Africa of the European Carp (*Cyprinus* sp.) in some parts seriously affected our inland fisheries resources. As a result of their omnivorous feeding habits, rapid propagation and tenacity of life, Carp spread rapidly, ruining waters by destroying vegetation, disturbing the bottom, and in severe cases rendering the water so foul as to make it unfit for consumption by stock. Rivers, farm dams, municipal and irrigation reservoirs became overpopulated with these fish, with the result that subsequent introduction of valuable table and sporting fish, such as the American Largemouth Bass (*Huro salmoides*), Smallmouth Bass (*Micropterus dolomieu*) and Spotted Bass (*Micropterus punctulatus*), proved unsuccessful. Waters, including trout rivers, which had formerly supported a good fish population were ruined when Carp gained access.

Various methods are known for the removal of fish from a water, but their application is, in most cases, limited. Netting is practicable only in small dams and, even then, it is impossible to remove all the fish. The most successful method of removing fish from a water is by emptying, but such a procedure is not feasible in the case of large impoundments such as lakes and irrigation dams. Dynamiting of waters is a highly technical and expensive operation, possible in isolated cases only. There remains a last method, that of inorganic and organic fish poisons. This method is the most satisfactory, but can only be carried out under expert supervision.

Inorganic fish poisons, such as copper sulphate and arsenical compounds, have successfully been used, but have the great disadvantage of being extremely poisonous to stock and human beings. Furthermore, waters treated with these poisons remain toxic over long periods, and aquatic vegetation and fish-food organisms are largely eliminated. On the other hand, organic fish poisons, such as Derris root (*Dequelia elliptica*), are temporary in effect, appear to be harmless to stock and human beings at concentrations lethal to fish and, at the same time, do not affect aquatic plants, while only some fish-food organisms are slightly susceptible. American workers have successfully used powdered Derris root with a standardised rotenone content of 5 per cent. in poisoning fish for the purpose of population studies.

In a previous report on "The Eradication of Fish from Open Waters by Means of Piscicidal Plants" (Annual Report of the Inland Fisheries Department, C.P., for 1947), it had been indicated that, of those plants tested, the use of the plant *Tephrosia Vogelii*, Hooker, promised to give the most satisfactory results as a fish poison. This report deals with experiments on the toxicity of the seed of *Tephrosia Vogelii* to freshwater fish.

The plant *Tephrosia Vogelii*, Hooker (Leguminosae), is widely distributed in the regions Nyasaland, Rhodesia, Portuguese East Africa, Belgian Congo, Transvaal and Natal. It is well known to the natives as an effective fish poison and is actually cultivated for this purpose. By pounding the roots and leaves of this plant and throwing the macerated tissues in the water, the natives stupefy and kill the fish, which can then easily be collected. Fish killed in this way can be eaten without any ill effect. During the course of the investigation reported below, several large fish killed with the seed of *Tephrosia Vogelii* were eaten by native labourers without any harmful effect.

The Toxic Principles of the Plant *Tephrosia Vogelii*, Hooker.

The isolation of the active principles from the leaves and seeds of *Tephrosia Vogelii* has been accomplished by several investigators in this field. The following information is quoted from D. G. Steyn, "The Toxicology of Plants in South Africa" (1934).

Hanriot (Czapek, 1913) isolated tephrosal ($C_{19}H_{16}O$) and tephrosin ($C_{31}H_{36}O_{10}$) from the leaves of the plant.

Preiss (Editorial, 1915) confirmed the presence of tephrosin in the plant obtained from Amani, Kenya Colony, and the same active principle was isolated in colourless crystals from the leaves and seeds obtained from Rhodesia. The seeds contained 0·3 per cent. tephrosin.

Wehmer (1929) states that the leaves contain an oily, volatile substance,

tephrosal, a crystalline neutral substance, tephrosin, and a yellow substance. He adds that tephrosin is a specific fish poison, and that the slight toxicity of the other two substances mentioned above is, perhaps, due to being contaminated with tephrosin.

According to Clark (1931), dequelin, which is highly toxic to fish, is contained in the leaves of *Cracca* (*Tephrosia*) *Vogelii*. Dequelin is a dimethoxylactone ($C_{23}H_{22}O_6$), which is pale green in colour, crystallises in rod-like plates and melts at 171° C.

Clark (1931*a*) in a later paper states that he studied the active principles in the leaves of *Cracca Vogelii* from Africa and Sumatra. He isolated a pharmacologically active crystalline substance corresponding to that obtained by Hanriot. This substance consisted of a mixture of two compounds, namely dequelin, with a melting-point of 171° C., and a colourless crystalline substance with a melting-point of 197°–198° C. Clark considers that Hanriot's tephrosin is a mixture of these two substances, and proposes that the name tephrosin be retained for the compound melting at 197°–198° C. He states that tephrosin is a hydroxydequelin.

Merz (1932) isolated about 0·3 per cent. of a mixed crystalline substance, which proved to be very toxic to fish and earthworms, from the seed of *T. Vogelii*, and states that it is a mixture of tephrosin, dehydrodequelin and probably dequelin.

According to information obtained from a publication by the Imperial Institute (Editorial, 1915), fish placed in dilute solutions of tephrosin exhibited great excitement followed by depression and decreased activity. The fish become paralysed, and ultimately turn over and die. Tephrosin, in a dilution of one in fifty million, was the minimum strength having fatal results. One in ten million caused fish to turn over in from five to seven minutes, death occurring in from fifteen minutes to one hour. Freshwater fish were found to be more susceptible to the effects of tephrosin than saltwater fish. It is stated that rabbits eat the leaves of the plant with impunity, and that dogs, which had received up to 1·0 gm. of tephrosin mixed in their food, showed no ill effects.

The Imperial Institute (Bull. Imp. Inst., 1915, xiii, 61) has confirmed Hanriot's chemical work, and found that the leaf yields 0·15 per cent. tephrosin, 0·06 per cent. tephrosal, and 0·05 per cent. of the yellow substance. The seeds yield 12 per cent. of a thick, brown, fixed oil and 0·3 per cent. tephrosin.

It would appear from the above data that the actual toxic principle in the seeds of *T. Vogelii* is the substance tephrosin ($C_{31}H_{36}O_{10}$) as determined by Hanriot. It also seems likely that waters treated with *T. Vogelii* will not harm human beings or stock drinking such water.

Experimental Methods.

Preparation of the Test Material.—The dry seeds of *T. Vogelii* used in this investigation were obtained from the Belgian Congo. The kidney-shaped seeds, about 5 mm. in length, possess a tough, brittle seed coat, black in colour, which encloses a yellowish endosperm and embryo. In order to obtain as uniform a sample as possible for testing, the seeds were ground to a fine powder. Further fractionation was obtained by passing the material through sieves ranging from 20 to 60 meshes per square inch. The following is an analysis of the ground seed material after it had been passed through sieves of 20 to 60 meshes per square inch. Weights and percentages are recorded as those portions which do not pass each consecutive sieve.

Mesh.	Weight in gm.	Percentage.
20 per square inch . .	2·9	1·1
30 ,, ,, ,, . .	32·9	13·1
40 ,, ,, ,, . .	48·6	19·3
50 ,, ,, ,, . .	33·2	13·2
60 ,, ,, ,, . .	133·4	53·2
	251 gm.	99·9

The first fraction mainly consists of parts of the seed coat and a few larger pieces of endosperm, whereas the following successive fractions contain progressively less seed coat material with a larger percentage of endosperm. The final fraction consists for the most part of endosperm only. *The final fraction which passed the 60-mesh-per-square-inch sieve was employed in all the experimental work reported below.*

Selection of a Test Fish.—The use of the common Goldfish (*Carassius auratus*) for studies in toxicity is well recognised. Initially goldfish were employed in this investigation, but determinations with this fish revealed so great a variation in susceptibility to *Tephrosia* poisoning that reliable results could only be obtained by performing a relatively large number of determinations in order to obtain a consistent mean result. Consequently, it was decided to employ the introduced North American Bluegill Sunfish (*Lepomis macrochirus*) as test animal. Far more reliable results were obtained with these fish, as their reactions and resistance to the poison were remarkably constant. The actual fish used in this investigation were bred and reared at the Jonkershoek Inland Fish Hatchery, and were held under

more or less identical conditions in a concrete tank, with a constant flow of water. The fish were fed daily on minced liver.

In this investigation, the point of death of the fish was taken as the criterion of toxicity.

The behaviour of Bluegill Sunfish when exposed to *Tephrosia* poisoning is of a more or less uniform type. The first visible indication that the poison is taking effect appears when the fish break the surface of the water, evidently experiencing difficulty in breathing. This is followed by loss of equilibrium, accompanied by wild unco-ordinated bursts of activity. The fish eventually slowly sink to the bottom, where they come to rest on their sides, or remain inertly floating just below the surface of the water. These convulsive movements, accompanied by stiffening of the body, continue at successively longer intervals, until the fish finally comes to rest, the only signs of life being feeble spasmodic movements of the gill covers. The actual point of death was determined by keeping the fish under close observation during the final stages, when only an occasional movement of the gill covers could be perceived. As these opercular movements became more feeble and erratic, the time was noted whenever the gill covers moved. When movement ceased for more than one minute the fish was recorded as being dead. After another 3 to 4 minutes the fish were again examined. Upon detecting further movement of the gill covers, observations were resumed as previously indicated. In this way the final point of death could be determined with considerable accuracy. With few exceptions, after removal of the fish at this stage there appeared to be no signs of life.

It is probable that *Tephrosia* poisoning of fish is similar in effect to that of rotenone, the toxic principle of Derris root (*Dequelia elliptica*). The impairment of the respiratory function appears to be the chief cause of death. According to Daneel (1933), quoted from Leonard (1938), histological examination of the gill filaments of fish killed by Derris root demonstrated a withering and breaking down of the gill epithelium. This was confirmed in the case of Bluegill Sunfish which had been subjected to *Tephrosia* poisoning. Histological examination of the gill filaments of these fish clearly indicated a pronounced withering of the gill filaments.

Experimental Procedure.

Except where otherwise indicated, all determinations described below were conducted in 8-litre jars suspended in a large aquarium of 500-litre capacity fitted with heaters. By means of a thermostat the water in the aquarium could be controlled, thus maintaining the water in all jars at a constant temperature. All determinations were carried out with filtered water derived from the Jonkershoek Hatchery water supply. This water

has a mean pH value of 6·8, and the oxygen content can be taken as varying between 6 to 7 p.p.m.

In the execution of each determination, the jars were filled with 6 litres of water each and suspended in the large aquarium until the temperature remained constant. The powdered seed was added, thoroughly mixed with the water by stirring, and allowed to soak for half an hour before the test fish were introduced. All determinations were carried out in duplicate, and two test fish were introduced into each jar. The survival times, loss of equilibrium and sizes of fish are recorded as the mean value for four test fish. When necessary, controls were run simultaneously. The test fish employed were carefully selected with regard to size and condition. Concentrations are expressed as parts of powdered seed per million parts of water by weight.

Experimental Results.

1. The toxic effect of powdered *Tephrosia Vogelii* seed on Bluegill Sunfish (*Lepomis macrochirus*) and Largemouth Bass (*Huro salmoides*).

In Tables I and II, the survival times of Bluegill Sunfish and Largemouth Bass are recorded when subjected to poisoning by concentrations of powdered *T. Vogelii* seed ranging between 1 to 100 p.p.m. at a constant temperature of 70° F. In order to obtain a clearer illustration of the above data, the results are graphically represented in figs. 1 and 2 according to a method employed by Powers (1917). The concentrations in p.p.m. are plotted as abscissa and the survival times as ordinate. Light circles are located from actual values obtained by experiment, and a curve is obtained, designated by Powers (1917) as the survival-time curve. From an examination of these curves it will be noted that the survival times of both Bluegill Sunfish and Largemouth Bass are not inversely proportional to the concentration of the *Tephrosia* seed. That portion of the curves between concentrations of 25 to 80 p.p.m. in the case of Bluegill Sunfish and 40 to 100 p.p.m. in the case of Largemouth Bass approaches a straight line, and clearly indicates that the survival times of Bluegill Sunfish and Largemouth Bass remain practically constant at concentrations above 25 and 40 p.p.m. respectively.

At lower concentrations, *i.e.* between 25 and 1 p.p.m. and 40 and 1 p.p.m. respectively, there is a proportionately greater increase in survival time with decrease in concentration. As illustrated by Powers (1917), a reciprocal curve of the survival time can be drawn, which is termed the velocity of fatality curve. The reciprocal is taken as $\frac{100}{\text{survival time}}$ and is plotted as

TABLE I.—BLUEGILL SUNFISH.

Temperature, 70° F.

Concentration in p.p.m.	Average survival time in minutes.	Average standard length in inches.
1·0	No effect	..
2·0	267	3·0
3·0	86	2·6
4·0	61	3·2
5·0	40	2·7
10·0	35	2·9
15·0	25	2·7
25·0	23	2·8
30·0	22	3·0
40·0	20	3·1
50·0	21	3·2
60·0	20	3·4
70·0	20	3·2
80·0	19	3·1

TABLE II.—LARGEMOUTH BASS.

Temperature, 70° F.

Concentration in p.p.m.	Average survival time in minutes.	Average standard length in inches.
1·0	No effect	..
2·0	187	2·5
5·0	58	2·6
10·0	32	3·2
15·0	31	2·4
20·0	22	2·6
30·0	20	2·5
35·0	21	3·2
40·0	14	2·4
50·0	13	2·6
60·0	12	2·3
80·0	15	3·5
100·0	15	3·3

one block ordinate per unit reciprocal. The concentration in p.p.m. is plotted as in the survival-time curve. In figs. 1 and 2 dark circles represent the reciprocals, and velocity of fatality curves are obtained. By extending

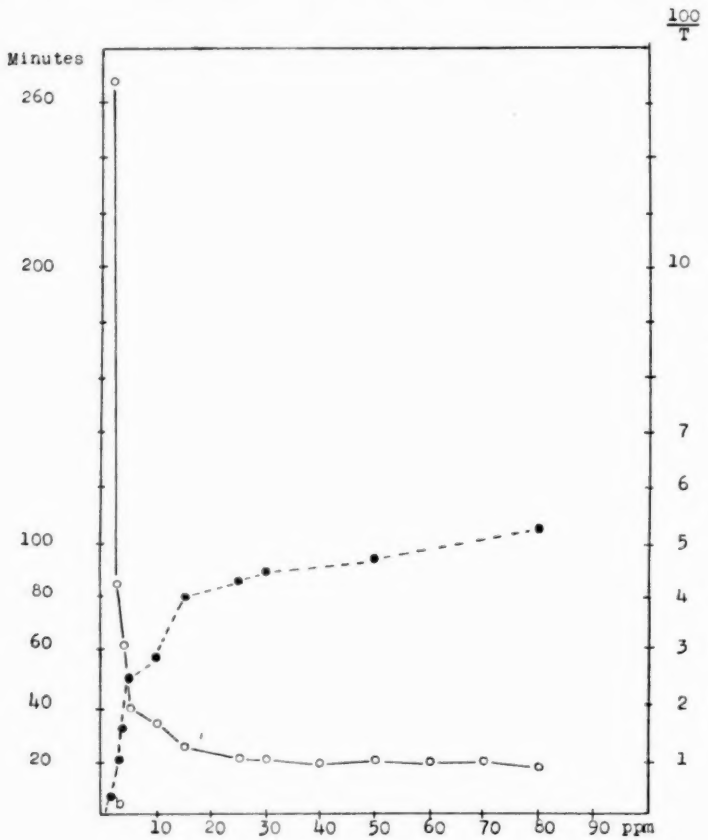

FIG. 1.—Bluegill Sunfish.

these curves the X-axis is cut at points B, which have been designated by Powers (1917) as the actual threshold of toxicity concentrations. It will be noted that the threshold of toxicity in the case of both Bluegill Sunfish and Largemouth Bass lies between 1 and 2 p.p.m.; *i.e.* below this lethal limit, powdered *Tephrosia Vogelii* seed which passes sieves of 60 meshes per inch is not toxic to Bluegill Sunfish or Largemouth Bass.

A comparison of the survival times of Bluegill Sunfish and Largemouth Bass reveals toxic effects of the same degree, except that Largemouth Bass are more susceptible to the poison as shown by lower survival-time values.

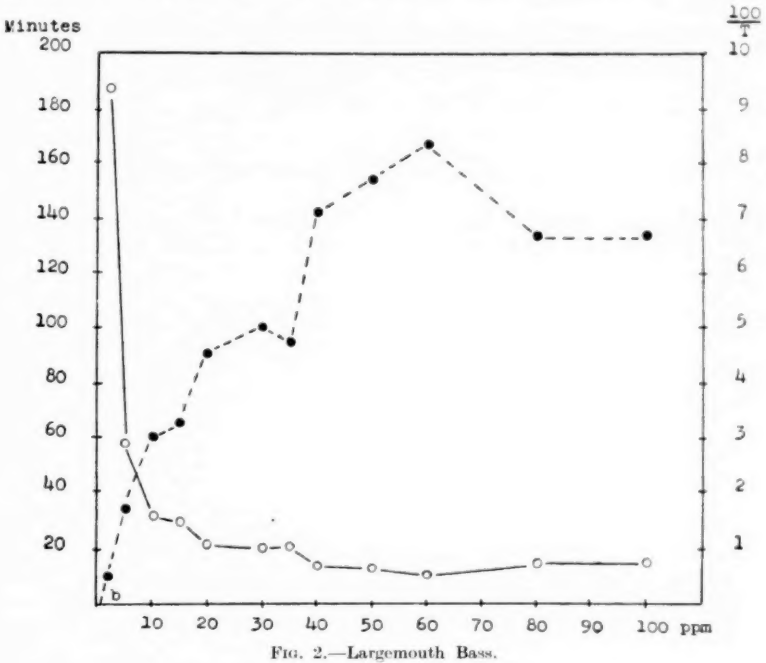

FIG. 2.—Largemouth Bass.

2. The toxic effect of powdered *Tephrosia Vogelii* seed on various divergent varieties of fish.

In order to determine the possibilities of employing the seed of *T. Vogelii* as a selective poison, the following divergent varieties of freshwater fish were subjected to tests at concentrations of 30, 10, 5 and 2 p.p.m. They are the common Goldfish (*Carassius auratus*), Largemouth Bass (*Huro salmoides*), Smallmouth Bass (*Micropterus dolomieu*), Barred Kurper (*Tilapia sparrmanii*), Top-minnow (*Gambusia holbrooki*) and Brown Trout (*Salmo fario*). All the test fish employed were bred and reared at the Jonkershoek Hatchery and, as far as possible, fish of the same size were selected.

In Table III, the average survival times, times of loss of equilibrium and weights of fish in gm. are recorded at concentrations of 30, 10, 5 and 2 p.p.m.

TABLE III.

Temperature, 60° F.

	Loss of equilibrium in minutes.				Survival times in minutes.				Weight of fish in gm.			
Concentration, p.p.m.	30	10	5	2	30	10	5	2	30	10	5	2
Goldfish . .	300	420	..	..	960	600	..	..	8	8	..	..
Largemouth Bass	10	11	15	45	20	31	58	180	8	10	7	6
Smallmouth Bass	9	10	30	60	31	40	105	390	7	12	10	4
Barred Kurper .	9	10	..	..	42	50	..	..	7	4	..	..
Gambusia . .	..	..	..	..	..	..	..	..	..	..	..	..
Brown Trout .	8	11	15	30	30	45	57	65	7·5	8	9	10

It will be noted that at concentrations of 30 to 2 p.p.m. the powdered seed of *T. Vogelii* is lethal to Brown Trout, Largemouth Bass and Smallmouth Bass, whereas concentrations of 5 p.p.m. and 2 p.p.m. have no toxic effect on Goldfish and Barred Kurper. Furthermore, it appears that *Gambusia holbrooki* are not in any way affected. These fish showed no signs of distress, and one female actually produced seventeen young while subjected to *Tephrosia* poisoning at a concentration of 30 p.p.m. The young fry, as well, appeared to suffer no ill effect from the poison. Several further tests with *Gambusia holbrooki* were carried out at concentrations of 100 to 200 p.p.m., with negative results. The apparent immunity of these fish warrants further investigation.

The above results illustrate that the seed of *T. Vogelii* may possibly be used as a selective fish poison in the case of mixed communities provided the threshold of toxicity of each variety of fish is known. There should be a relatively large margin between the threshold of toxicity values for each variety of fish or group of fishes, as the effect of factors such as temperature, size of fish and type of water will markedly influence the threshold of toxicity.

An indication of the comparative toxicities of *Tephrosia* poisoning to the fish tested can be deduced from an examination of the survival times.

Largemouth Bass and Smallmouth Bass are susceptible to the same degree, whereas the Barred Kurper is more resistant to the poison, and Goldfish is the hardiest. As could be expected, Brown Trout were the most susceptible to the poison.

As an example of selective poisoning, a Largemouth Bass, Smallmouth Bass, Barred Kurper and Goldfish community may be taken. Such a

community, when exposed to poisoning by powdered *Tephrosia* seed at a concentration of 2 to 3 p.p.m., may result in the eradication of Largemouth and Smallmouth Bass without any harmful effect on the Barred Kurper or Goldfish.

3. Temperature and its effect on the toxicity of *Tephrosia Vogelii* seed to Bluegill Sunfish (*Lepomis macrochirus*).

The inhibitory or stimulating effect of changes in temperature on the general metabolism and activity of freshwater fish is well known. The above data recorded in Table IV illustrate the influence of temperature on the toxicity of powdered *Tephrosia* seed on Bluegill Sunfish at a constant concentration of 30 p.p.m. Determinations were made at 5° intervals from 50° to 90° F. During each test, compressed air was diffused through the test solution in order to obviate the effect of an oxygen deficiency which might affect the survival time. The harmful effect of sudden changes in temperature was compensated for by slowly bringing the test fish up to the required temperature before introducing them into the test solutions. Above 90° F. the fish in controls showed obvious signs of distress resulting in loss of equilibrium, but recovered when the temperature was lowered.

TABLE IV.

Concentration of *Tephrosia* seed, 30 p.p.m.

Temperature, °F.	Average survival time in minutes.	Average standard length in inches.
50	48	2·7
55	39	3·0
60	33	3·0
65	30	3·1
70	17	2·7
75	17	3·1
80	12	3·2
85	11	3·4
90	9	3·0

The results show a gradual decrease in survival time with increase in temperature, or *vice versa*. There is a sudden drop in survival time between 65° and 75° F. An increase in temperature of 40° F. results in a decrease in survival time of 39 minutes. From a point of view of general metabolism, the optimum temperature for Bluegill Sunfish appears to lie between

50° and 70° F. where the effect of changes in temperature on toxicity are most pronounced. The importance of rigid temperature control in toxicity experiments is obvious. Similarly, when carrying out field experiments, the efficacy of the poison will be influenced by the season, *i.e.* water temperature.

4. The toxic effect of powdered *Tephrosia Vogelii* seed on Bluegill Sunfish (*Lepomis macrochirus*) of different sizes.

In Table V, the survival times recorded are obtained with Bluegill Sunfish ranging in size from ·85 gm. in weight up to 145·8 gm. when exposed to poisoning by powdered *Tephrosia* seed at 30 p.p.m. The results indicate low survival-time values between the sizes ·85 to 10·1 gm., whereas these values are practically doubled between the sizes 24 to 145·8 gm. It will be noted that the survival times remain more or less constant between the sizes 24 to 145·8 gm., the maximum variation being 8 minutes. The total difference in survival time between the sizes ·85 to 145·8 gm. is 29 minutes. These results indicate the importance in toxicity determinations of using test fish of approximately uniform size and condition, as well as the necessity of duplication of tests in order to arrive at a reliable mean result.

TABLE V.

Temperature, 65° F. Concentration, 30 p.p.m.

Average weight of fish in gm.	Average survival time in minutes.	Average time of loss of equilibrium.
0·85	19	9
2·0	20	9
10·1	24	9
24·0	30	8
34·0	40	10
40·0	33	8
60·0	42	10
72·7	33	7
78·0	43	12
145·8	48	15

5. The rate of dissipation of the toxic principles contained in the seed of *Tephrosia Vogelii*.

The dissipation, if any, of a fish poison after its introduction into a water is of great practical importance to the fish culturist, as the period of effective-

ness of the poison determines the time at which the water may be restocked with safety, as well as its palatability for domestic purposes and the watering of stock.

The following results (Table VI) were obtained by subjecting Bluegill Sunfish to *Tephrosia* seed poisoning at a concentration of 30 p.p.m. at 24-hour intervals. The test fish were not introduced into the same test solution at consecutive intervals but into separate solutions of different ages, thus obviating changes in concentration of the test solution due to absorption of a certain percentage of the poison by the test fish.

TABLE VI.

Concentration, 30 p.p.m. Temperature, 65° F.

Time lapse in hours.	Average survival time in minutes.	Average standard length in inches.
24	34	3·0
48	46	3·8
72	38	3·3
96	44	3·3
120	40	3·9
144	..	..
168	..	..

The results show that the survival time remains practically constant from 24 hours up to 120 hours after introduction of the poison. At 144 hours and after, the poison appears to be entirely dissipated. This sudden drop in toxicity was further investigated by repeated determinations at 120 hours and 144 hours, and in all cases the fish died at 120 hours but appeared to suffer no ill effect at 144 hours. It may therefore safely be stated that the seed of *Tephrosia Vogelii* is not toxic to Bluegill Sunfish 6 days after its application. This time limit will probably vary with different varieties of fish, and will be influenced by the size of the fish, temperature, and its use under natural conditions. However, it may be safely assumed that a water which had been treated with the seed of *T. Vogelii* could be restocked with safety and prove palatable after a 15- to 20-day interval.

6. The toxic effect of powdered *Tephrosia Vogelii* seed on some fish food organisms.

In selecting a fish poison, an important consideration is the effect it will have on the aquatic flora and fauna of a water. It is obviously advantageous

to use a poison lethal to fish but not toxic to fish food organisms or aquatic plants. Waters treated with such poisons could be restocked immediately the poison had become dissipated. On the other hand, partial or complete eradication of fish food organisms and aquatic plants will necessitate their being re-established before restocking could be successfully attempted. Furthermore, some phase of the aquatic flora and fauna may be entirely eradicated, and result in the removal of an essential link in the normal food chain characteristic of a particular water.

The effect of powdered *Tephrosia* seed on some important fish food organisms at concentrations of 10 and 30 p.p.m. are recorded in Table VII.

TABLE VII.

Temperature, 65° F.

Food organisms.	Average survival time.	
Concentration:	10 p.p.m.	30 p.p.m.
Platanna—*Xenopus laevis*—adults	..	..
Platanna—*Xenopus laevis*—tadpoles	..	6 hours
Water Flea—*Daphnia magna*	3½ hours	1 hour
Backswimmer—*Notonecta* sp.	..	..
Bloodworms—*Chironomus* sp.—larvae	..	..
Aquatic Snails—*Lymnaea* sp.	..	..
Dragonfly Larvae	..	..
Water Beetle—*Dytiscus* sp.	..	..
Mosquito Larvae—*Culex* sp.	..	..
Freshwater Crab—*Potamonautes* sp.	..	32 hours
Freshwater Shrimp—*Gammarus* sp.	..	10 „

It is significant that only four of the organisms were affected at a concentration of 30 p.p.m. and one organism at 10 p.p.m. The susceptibility to *Tephrosia* poisoning of the tadpoles of *Xenopus laevis*, the Water Flea, *Daphnia magna*, the Freshwater Crab. *Potamonautes*, and the Freshwater Shrimp, *Gammarus*, must be ascribed to the fact that they all possess gills, whereas all the other organisms tested breathe air directly. These findings further substantiate the belief that the toxicity of *Tephrosia* seed is primarily due to its action on the gills, causing the fish to gradually suffocate.

From the above results it will be noted that at a concentration of 10 p.p.m. only the Water Flea, *Daphnia magna*, succumbed to *Tephrosia* poisoning. It seems likely, therefore, that at 10 p.p.m.—a concentration which will probably prove lethal to most freshwater fish—the effect of the

poison will be negligible on most fish food organisms and, if at all effective, only in those cases where such organisms possess gills.

7. A field test employing the powdered seed of *Tephrosia Vogelii* as a fish poison.

A small earth pond used as a rearing pond at the Jonkershoek Inland Fish Hatchery was selected for the purpose of conducting an experiment under natural conditions. This pond when full has an average depth of 2 feet 6 inches, a mud bottom, and was covered at the time of the experiment with an aquatic plant community consisting of *Sagittaria sagittifolia*, *Lagorosiphon muscoides* and *Limnanthemum thunbergianum*. Sixteen days before introducing the poison the following freshwater fish were introduced into the pond. Weights given in brackets indicate the average weight of the fish.

3 Carp (*Cyprinus carpio*) (2 lb. 2 oz.).
3 Bluegill Sunfish (*Lepomis macrochirus*) (8 oz.).
3 Largemouth Bass (*Huro salmoides*) (3 oz.).
3 Spotted Bass (*Micropterus punctulatus*) (3 oz.).
3 Goldfish (*Carassius auratus*) (1 oz.).
3 Barred Kurper (*Tilapia sparrmanii*).
2 Tench (*Tinca vulgaris*) (8 oz.).
2 Wit fish (*Barbus andrewi*) (1 lb.).
1 Cape Kurper (*Sandelia capensis*) (1 oz.).

At 9 a.m. on 11th June 1948, when the poison was introduced, the surface temperature of the water was 54° F., pH 6·4, and the dissolved oxygen content 6·4 p.p.m. The volume of water in the pond amounted to approximately 3600 cubic feet or 26,930 gallons, which would require the addition of 2·246 lb. or 1·019 kg. powdered *Tephrosia* seed in order to obtain a concentration of 10 p.p.m. In actual fact, exactly 1 kg. of powdered seed was introduced in the execution of this experiment, which for practical purposes provided for an approximate concentration of 10 p.p.m. The powdered *Tephrosia* seed was applied by hand, spreading it over the entire surface of the pond. It was found, however, that a large percentage of the powder remained floating on the water surface, and water had to be sprayed over the surface, which effectively precipitated the powder, the greater part of which sank to the bottom, whereas the finer particles remained in suspension. Approximately one hour after introducing the poison, the first fish to show signs of distress were the Wit fish, followed by the Bass, Bluegill Sunfish and, finally, the Carp. None of the other fish showed up, and could not be seen due to the discoloration of the water. Approximate survival times could not be determined, as most of the fish

remained at the bottom prior to death. Some, however, sought the shallows, and at times actually tried to leave the water. At 9 a.m. the next morning, *i.e.* 24 hours after applying the poison, the pond was completely drained. Of the 23 fish originally introduced only the 3 Barred Kurper remained alive. These fish were obviously distressed and had lost equilibrium, but recovered completely when placed in fresh water. It is reasonable to suppose that the Barred Kurper would have died if exposed to the poison over a longer period. The tolerance of these fish to *Tephrosia* poisoning under natural conditions warrants further investigation.

The complete kill of all fish, including the tenacious Carp, proves beyond doubt that the powdered seed of *T. Vogelii* could be successfully used as a freshwater-fish poison. Its use in South Africa as an effective means of eradicating Carp is advocated.

It is recommended that the following procedure be adopted when attempting the eradication of undesirable species of freshwater fish from open waters:—

1. The seed of *T. Vogelii* should, first of all, be ground to a fine powder in order to facilitate leaching of the poison.

2. The volume of water to be treated should be determined as accurately as possible.

3. When a complete kill of all fish is desired, the amount of powdered *Tephrosia* seed to be applied should be sufficient to allow for a concentration of between 10 to 20 p.p.m. by weight.

4. The use of this poison during summer will be more effective and is, therefore, preferable.

5. The powdered seed should be broadcast over the entire water surface on a calm day.

6. As a large percentage of the powdered seed tends to remain floating at the water surface, some means of precipitating the poison must be found. It is suggested that the powdered seed could be applied by means of a spray pump after mixing the powder with a small amount of water. Spraying could be carried out by wading in the shallows and from a boat in deep water. When large impoundments are to be treated, the powder could be released from a boat in the wake of an outboard motor.

7. As the fish are stupefied by the poison and tend to collect in the shallows and at the water surface, attempts should be made to remove as many fish as possible by means of hand nets. All fish not removed will decompose and, if sufficiently numerous, lead to pollution of the water.

8. Fish removed while still fresh can be eaten without any harm to the consumer.

9. Restocking of the water can be carried out with safety 15 to 20 days after treatment.

SUMMARY.

1. Laboratory tests show that powdered *Tephrosia Vogelii* seed standardised to pass a 60-mesh-per-square-inch sieve is lethal to Bluegill Sunfish (*Lepomis macrochirus*) and Largemouth Bass (*Huro salmoides*) at and above a concentration of 2 p.p.m. at 70° F. The threshold of toxicity for both species lies between 1 and 2 p.p.m.

2. The possibility of employing *Tephrosia* seed as a selective poison is suggested, provided the threshold of toxicity is known for each variety of fish in a single community.

3. Temperature has a marked influence on the toxicity of *Tephrosia* seed. An increase in temperature of 40° F. results in a decrease in survival time for Bluegill Sunfish of 39 minutes.

4. The toxicity of *Tephrosia* seed varies with the size of the fish. With increase in size, the fish are progressively less susceptible to the poison up to a certain size limit.

5. Dissipation of the powdered seed is rapid, being ineffective 144 hours after its application.

6. Fish food organisms will suffer no appreciable ill effect at concentrations of *Tephrosia* seed lethal to most freshwater fish.

7. A field test is described proving the effectiveness of powdered *Tephrosia* seed as a freshwater fish poison.

8. It is suggested that the seed of *Tephrosia Vogelii* could be effectively employed for the purpose of eradicating Carp.

9. The procedure to be followed when applied in the field is explained.

ADDENDUM.

At the end of 1948 a further field test was carried out at the Jonkershoek Hatchery on a pond which had been stocked with six carp (*Cyprinus carpio*) breeders, approximately 2 lb. each. These fish had been introduced into the pond about three months earlier, for breeding purposes, in connection with these experiments. It was decided to eradicate the entire population of the pond by employing the powdered seed of the plant *Tephrosia Vogelii* as a further test of its efficacy.

The approximate volume of the pond amounted to 6000 cubic feet, and powdered seed was added so as to produce a concentration of 10 p.p.m. in the pond. At the time of the tests the temperature of the water was 72° F., pH 7·0 and dissolved oxygen 8 p.p.m. (surface).

The poison was spread by hand over the entire water surface at 9.30 a.m. Approximately fifteen minutes after introducing the poison a large number of young carp, 1 to 1½ inches in length, appeared at the water surface showing obvious signs of distress. Half an hour later a large number of

young carp were floating dead at the water surface. The six large breeders in the pond were by this time behaving in a similar manner, and were all dead approximately five hours after application of the poison. Two days after, ten 9-inch Bluegill Sunfish (*Lepomis macrochirus*) were introduced into the pond, and were retrieved unaffected when the pond was emptied seven hours later. It would appear, therefore, that under natural conditions, in earth ponds, the poison rapidly becomes absorbed, thus not affecting fish introduced two days afterwards, whereas in the laboratory experiments previously reported, dissipation of the poison is slow, taking at least 144 hours. A few freshwater crabs and adult (*Xenopus*) frogs found in the pond after it had been emptied were apparently not affected by the poison.

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ON A COLLECTION OF SESSILE BARNACLES FROM KNYSNA ESTUARY, SOUTH AFRICA.

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(With Plate XI and two Text-figures.)

(Read February 1949.)

Introduction.

In July 1947, six members of the Zoology Department, University of Cape Town, undertook an investigation of the biology of Knysna Estuary, on the south coast of the Cape Province. During this period a representative collection of barnacles was made (*a*) from the shores of the estuary, where they were mostly found attached to stones, pylons, etc., and (*b*) from dredgings in the estuary itself. This collection was subsequently checked and added to by two members of the Department, who made a second visit to Knysna in November of the same year.

Apart from the typical marine barnacles which occur at the rocky Heads on either side of the mouth, there was found to be a rich estuarine population extending up 8½ miles of the estuary into a salinity as low as approximately 1·4 parts per 1000 (low-tide record, taken in July 1947).

The marine forms occurring near the mouth are typical of the littoral population of Southern Africa, and include *Tetraclita serrata* Darwin, *Chthamalus dentatus* Krauss, *Octomeris angulosa* Sowerby, and *Balanus trigonus* Darwin. *Balanus algicola* Pilsbry and *Balanus maxillaris* Gronovius were not actually collected from the Knysna coast-line, but have previously been recorded from Port Elizabeth and Mossel Bay, both of which are on the south coast, respectively east and west of Knysna.

Of these only a few specimens were able to survive the lower salinity of the estuary proper, and none played a conspicuous part in the fairly abundant Cirripede population present there.

This estuarine population was composed mainly of two species of barnacles, *Balanus amphitrite* Darwin and *Balanus elizabethae* Barnard, the former being far more numerous than the latter.

Balanus elizabethae was first described by Barnard (1924), who, however, had only three specimens at his disposal. Through the courtesy of

Dr. Barnard it was possible to establish the identification of the species by comparison with the type specimens, although unluckily the mouth-parts of the latter had been lost. The original description was found to be insufficient to cover the variation in the species and no text-figures were given; accordingly in this paper Barnard's original description has been expanded and text-figures have been included.

List of Species occurring in Estuary Proper.

Family BALANIDAE.

Balanus algicola Pilsbry 1916.

A few specimens only were obtained from dredgings opposite Thesen's wharf in the lower part of the estuary, in a minimum salinity of approximately 23·9 parts per 1000 (low tide, July 1947).

Balanus trigonus Darwin 1854.

A few specimens were taken from dredgings close to Leisure Isle and opposite Thesen's wharf, both in the lower part of the estuary, in a minimum salinity of approximately 23·9 parts per 1000 (low tide, July 1947).

Balanus amphitrite Darwin 1854, var. *denticulata* Broch 1927.

This is by far the most common species of barnacle in the estuary, occurring in salinities from below 21·7 parts per 1000 at low tide (July 1947) to close on that of sea-water. The barnacles are attached to any suitable substratum—stones, posts, pylons, etc.—and have even been found growing on grass stems. So far, however, they have not been recorded from the marine coast-line.

The colour is normally white, with longitudinal violet lines, and white or brownish-violet radii and opercular plates (Pl. XI, F). The radii frequently have a speckled appearance. The basal diameter reaches 2·6 cm. and the height 1·9 cm.

The characters of the specimens agree exactly with those described by Broch (1927) for *B. amphitrite*, var. *denticulata*, from the Suez Canal, except that the rostral plate is invariably convex, and not "almost always concave in profile" as in Broch's specimens. Most striking is the exact resemblance in the structure of the third cirrus and the large number of teeth on the labrum, both characters of systematic importance. Broch states in regard to the number of teeth on the labrum that "in the other varieties which have been studied in detail there are almost always 3 or seldom only 2 on each side". In the specimens from Knysna there are about 13–14 teeth on each side, extending right into the notch.

An interesting feature of this variety is that it occurs in two distinct forms in Knysna Estuary, which differ markedly externally but are exactly similar in the structure and arrangement of the mouth-parts and appendages.

In addition to the typical form described above with distinct coloration, a fairly tall shell and projecting opercular plates, there is another more squat and depressed form usually occurring at lower levels on the shore, in general giving the impression that it is subjected to greater wearing (Pl. XI, E). In this aberrant form the colour is usually dirty white, with the shell roughened and the violet stripes either absent altogether or only faintly visible near the base. The shell is very much lower, with a maximum height of 0·9 cm. The opercular plates are flatter and do not project through the orifice, and the tergal margin of the scutum has a typical notched appearance.

After much consideration it was decided that it would be impracticable to separate these two forms, since it is possible to select a complete series of intermediate types ranging from the flat whitish type with the notched scutum to the distinctly coloured tall type with the straight-edged scutum. The difference in appearance is possibly associated with the difference in habitat, those living at a lower level on the shore being more under the influence of water movements and drifting sand particles than those which are higher on the shore and submerged only at high tide. Pilsbry (1916) suggests that in some species the character of the scutum may be modified by wearing. In regard to *Balanus mirabilis* he says (p. 79) "the peculiarly hollowed-out tergal border of the scutum is due to erosion of the outer layer of the valve, and will not be present when unworn specimens are found". Such an erosion would also account for the fact that, in the aberrant form of var. *denticulata*, the opercular valves do not project through the orifice as they do in the typical form.

Balanus elizabethae Barnard 1924 (text-fig. 1 and Pl. XI, A–D).

Shell low-conical, covered with a thin almost colourless epidermis. Orifice diamond-shaped to pentagonal, only slightly notched.

Colour white and transparent, with no markings of any sort.

Basis calcareous, brittle, attached throughout, sparsely porous, smooth on inner surface, with deep pits round edge for insertion of internal ribs of parietes.

Parietes externally smooth, not porous, internally with regular strong ribs extending up to the sheath and crenulate at the base. Sheath very short, horizontally ribbed. Due to the transparent nature of the shell the internal ribs of the parietes are visible from without, causing an apparent striation.

Radii broad, summits normally at about 45° with base, but often nearly parallel to base, the edges crenulate, not porous.

Alae broad, summits only slightly oblique.

Scutum externally concave, tergal border slightly convex. Growth ridges moderately close, faint in upper portion, but distinct near base.

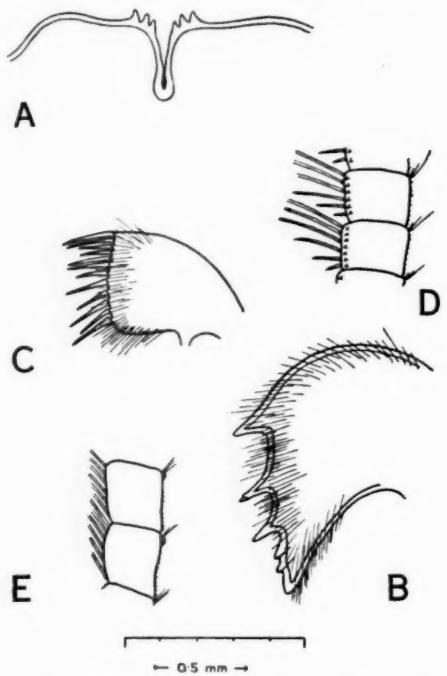

FIG. 1.—*Balanus elizabethae* Barnard. A, labrum; B, mandible; C, maxilla; D, two segments of 3rd cirrus; E, two segments of 5th cirrus.

Basal margin longer than tergal margin. Articular ridge very prominent, projecting over articular furrow. Adductor ridge short, pit for depressor muscle obsolete.

Tergum externally flat, with growth ridges very faint, and a shallow groove running towards the spur. Basal margin strongly concave between the prominent depressor muscle crests and the spur. Width of spur slightly under one-third that of basal margin, spur subtruncate, distinct from basiscutal angle. Articular ridge prominent and overhanging the upper part of the deep articular furrow. Apex blunt and corroded.

Labrum with 3 teeth on either side of notch, not 2 as stated by Barnard. Palpus with an irregular row of short pectinated bristles on labral face, and a dense cluster of long pectinated bristles at distal end.

Mandible with 1st to 3rd teeth acute and widely separated, 4th and 5th rudimentary, obtuse, but distinctly removed from subacute inner angle. 2nd tooth with a bifid point. Lower edge setose.

Maxilla with inner edge straight, with 10 to 16 spines, of which the first 2 are frequently but not always longer than the others. The most common number appears to be 11.

The length of the cirri varies considerably among individuals, and is obviously not of diagnostic value. The number of joints given in the following description indicates the range of variation within approximately a dozen specimens dissected. Of far more value for systematic purposes is the general appearance of the first cirrus, and the spinular structures on the 3rd.

First cirrus with anterior ramus about twice length of posterior. Anterior ramus 17–22 jointed, the lower 8 to 11 joints larger than the distal ones, pigmented, and protuberant anteriorly. Posterior ramus 9–11 jointed, very stout, about half as broad as long, tapering distally, all the joints broad, pigmented and protuberant anteriorly. Both rami bearing dense pectinate and plain bristles.

Second cirrus with rami sub-equal. Anterior ramus 12–17 jointed, basal joints slightly protuberant and darkly pigmented anteriorly, the last 3–5 joints smaller than the proximal ones and unpigmented. Posterior ramus 10–13 jointed, all joints slightly protuberant and darkly pigmented anteriorly. Both rami bearing dense pectinate and plain bristles.

Third cirrus with rami sub-equal and pedicel swollen and protuberant anteriorly. Anterior ramus 15–19 jointed, with about the first 11 joints bearing a number of small proximally directed, pointed tubercles on anterior margins, and minute distally directed spinules on posterior margins, in addition to usual bristles. Posterior ramus 12–18 jointed, with minute spinules on posterior margins of proximal joints in addition to usual bristles.

Fourth cirrus with rami sub-equal. Anterior ramus 25–40 jointed, posterior ramus 25–38 jointed. Proximal joints of both rami with minute spinules and 1 or 2 minute curved teeth on posterior borders in addition to usual bristles.

Fifth and sixth cirri with rami sub-equal and 33–42 jointed. Proximal joints with minute spinules and 1 or 2 minute curved teeth on posterior borders in addition to usual bristles.

Penis longer than posterior cirri, sparsely setose.

Size.—Maximum basal diameter, 1·9 cm.; maximum diameter of orifice, 1·0 cm.; maximum height, 1·2 cm.

Distribution.—Zwartkops River, Port Elizabeth (Barnard, 1924); Knysna Estuary.

Remarks.—In Knysna Estuary *Balanus elizabethae* occurs at approximately mid-tide level in salinities varying from about 1·4 parts per 1000 to almost that of sea-water. It appears to be a typical estuarine form, and has not been observed on the neighbouring coast amongst the marine fauna.

Barnard (1924) considered the species to be closely allied to *Balanus hesperius* Pilsbry, of the subgenus *Hesperibalanus*, but the porous nature of the basis, which was not known to Barnard, would seem to exclude it from the subgenus.

Balanus elizabethae is closely allied to *B. emkweniensis* Nilsson-Cantell (1932) from Pondoland, on the east coast of the Cape Province, the only significant difference being the presence of 3 pairs of teeth on the labrum in *B. elizabethae* and 2 in *B. emkweniensis*. If this too should prove to be a variable character, the latter species should certainly be included in *B. elizabethae*. Nilsson-Cantell considered his species most closely allied to the subgenus *Solidobalanus* of Pilsbry, but adds that it stands very much on its own.

Tetraclita serrata Darwin, 1854.

Only isolated specimens were found on the shores of the estuary in several localities as far up as the railway bridge, *i.e.* in salinities as low as approximately 23·9 parts per 1000 at low tide (July 1947).

Family CHTHAMALIDAE.

Chthamalus dentatus Krauss, 1848.

Isolated specimens were collected from various localities on the shores of the estuary as far up as Belvidere, in salinities slightly lower than 23·9 parts per 1000 at low tide (July 1947).

Summary and Conclusions.

The following sessile Cirripedes occur in Knysna Estuary in a salinity lower than that of sea-water:—

Fam. Balanidae.

Balanus algicola Pilsbry.
Balanus trigonus Darwin.
Balanus amphitrite, var. *denticulata* Broch.
Balanus elizabethae Barnard.
Tetraclita serrata Darwin.

Fam. CHTHAMALIDAE.

Chthalmus dentatus Krauss.

In addition *Octomeris angulosa* Sowerby occurs near the mouth amongst what can be considered to be typical marine fauna, and *Balanus maxillaris* Gronovius has at least been recorded from neighbouring localities.

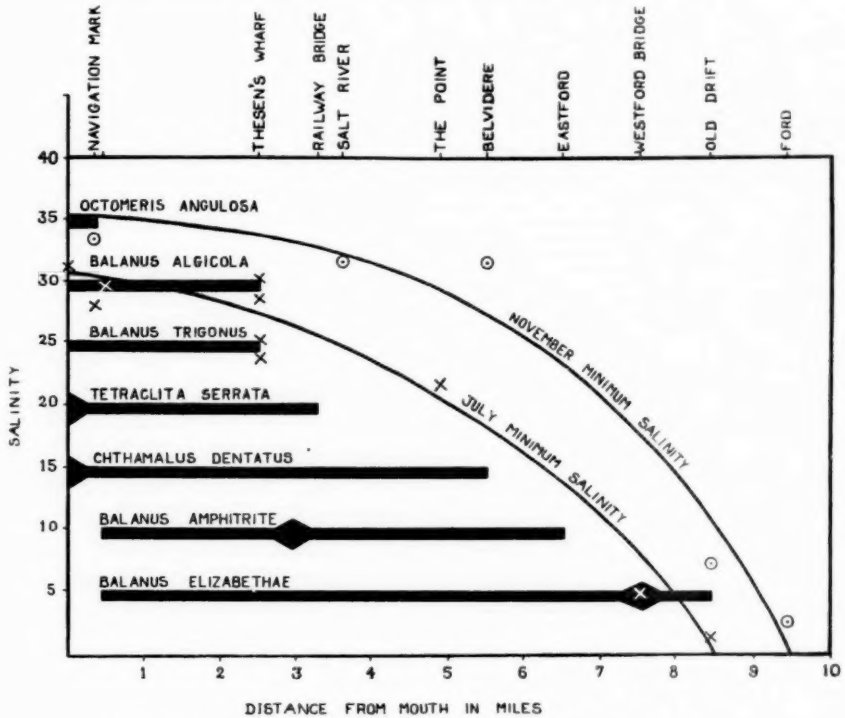

FIG. 2.—Diagram showing the distribution of the barnacles in Knysna Estuary. The salinities, in parts per 1000, as found in July and November 1947 are shown in the same diagram. The curves are drawn freehand as a guide to the eye.

The distribution of these barnacles along the 8½ miles which constitute the estuary proper is shown diagrammatically in text-fig. 2. Rough curves for the minimum salinities recorded in July and in November 1947 are included in the same diagram. The fact that the salinity curve for July (Winter) is lower than that for November (Summer) is in accordance with the fact that the former period has the greater rainfall.

B. algicola and *B. trigonus* were found only in dredgings in the estuary, and may of course have been washed in from the sea attached to floating seaweed, etc. The maximum depth from which these dredgings were obtained was 6 metres.

Of the marine barnacles, *Tetraclita serrata* and *Chthamalus dentatus* appear to be the most resistant to lowered salinities.

Balanus amphitrite, var. *denticulata*, and *Balanus elizabethae* are apparently typical estuarine forms not to be found close to the mouth, but forming the dominant members of the cirripede population throughout the estuary proper into extremely low salinities. *Balanus amphitrite*, var. *denticulata*, according to Pyefinch (private correspondence), is fairly widely distributed as a fouling organism on ships' hulls. It was originally reported by Broch from the Suez Canal, where the salinity is typically higher than that of normal sea-water, so it appears to be an extremely euryhaline form.

An attempt has been made in text-fig. 2 to show the regions of maximum abundance of the most important species by thickenings of the black lines, but this is of course only approximate.

How far this balanoid population is typical of South African estuaries in general cannot be ascertained at present, but will, it is hoped, become apparent in the course of further investigations which are now in progress.

Grateful acknowledgments are due to Dr. K. H. Barnard of the South African Museum for his co-operation, and to K. A. Pyefinch of the Marine Station, Millport, Scotland, for checking the identifications.

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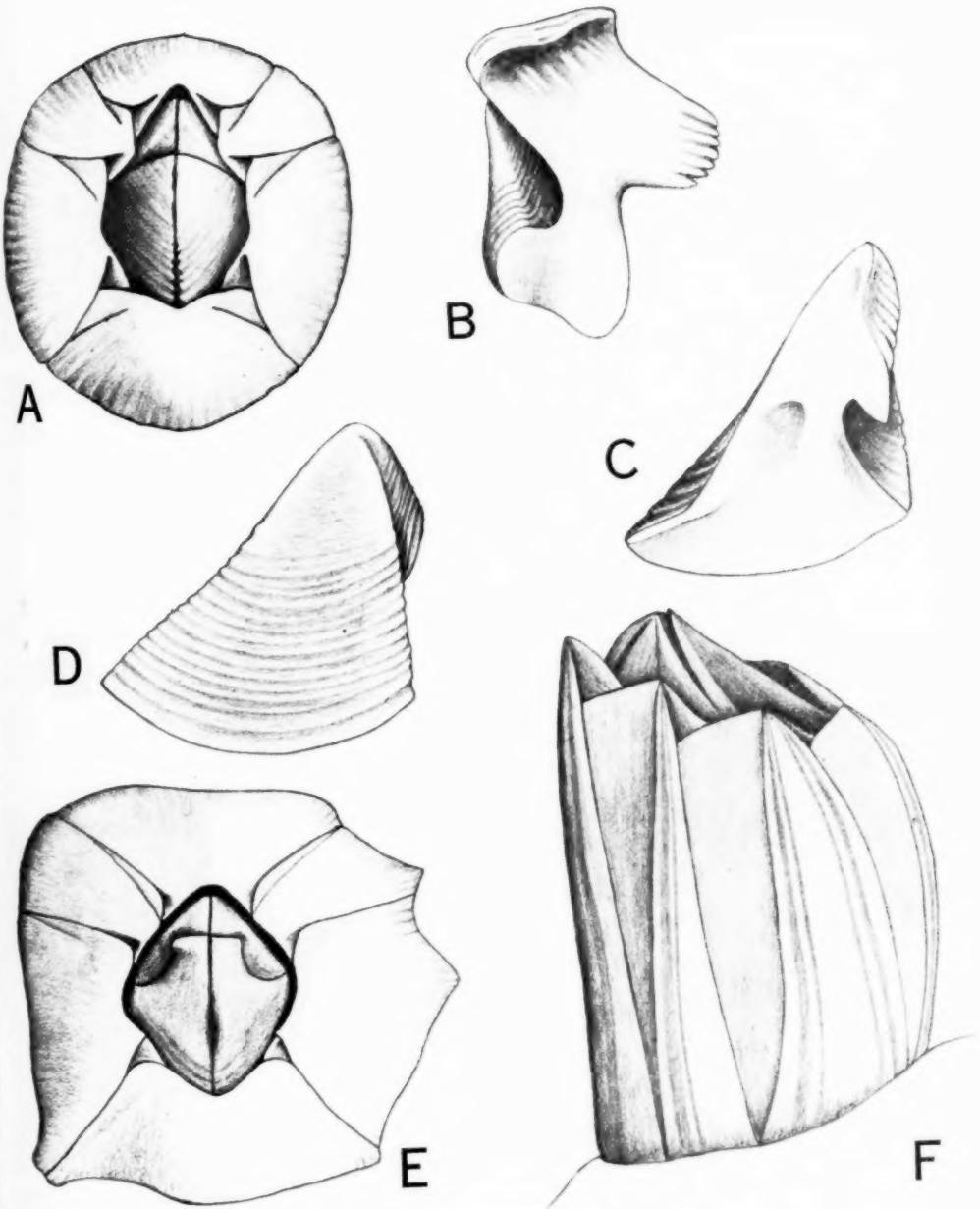

Naomi Millard. *Neill & Co., Ltd.*

DESCRIPTION OF PLATE.

FIGS. A–D, *Balanus elizabethae* Barnard. A, upper view of whole animal (×5·5); B, tergum, inner view (×11·2); C, scutum, inner view (×11·2); D, scutum, outer view (×11·2).

FIG. E, *Balanus amphitrite*, var. *denticulata* Broch. Squat, worn form with notched scutum (×4).

FIG. F, *Balanus amphitrite*, var. *denticulata* Broch. Tall form with straight-edged scutum (×4).

NOTES ON THE WHIP-SCORPIONS (PEDIPALPI) OF SOUTH AFRICA.

By R. F. Lawrence, Ph.D., Natal Museum, Pietermaritzburg.

(With six Text-figures.)

(Read March 16, 1949.)

Very little has been written about the South African Whip-scorpions, and few references to their habits and life-history are found in the literature, although the widespread species, *Damon variegatus* Perty, is a common arachnid in parts of Southern Africa, especially in the eastern half.

The South African Fauna.

Four species of Pedipalpi are known from South Africa, and up to very recently only the sub-order Amblypygi was considered to occur in the sub-region; in 1947, however, a single specimen of the sub-order Uropygi was found in a collection of Arachnida made by Dr. Ivar Trägardh in Natal and Zululand during 1904–5. This specimen, which represents a new species, *Schizomus zuluanus* (1), was taken at Dukuduku in Zululand; it is fairly closely related to *Schizomus montanus*, described by Hansen (3) from the slopes of Kilimanjaro.

The three remaining species of South African Pedipalpi all belong to the sub-order Amblypygi of tailless whip-scorpions. *Damon variegatus* is a widespread species in Africa, but has probably migrated from the tropics down the eastern half of Southern Africa; it is at the present time much more numerous in Natal and Zululand than in the Western Cape.

Phrynichus bacillifer (Gerst.) is now recorded for the first time from the South African region; though more properly an inhabitant of tropical East Africa (Zanzibar, Tanganyika) and Madagascar, it is represented by a single specimen from Bindura, Southern Rhodesia, in the collection of the National Museum of Southern Rhodesia, Bulawayo.

The fourth species, *Phrynichus scullyi*, was described by Purcell (5) in 1901, and seems to occupy a limited area in Little Namaqualand and the Western Cape districts of Clanwilliam and Calvinia. The distribution of the four South African species, based on material in the collections of the

various South African museums, is shown in text-fig. 1. The distribution of *Damon variegatus* in South Africa has been somewhat extended by its discovery in the northern districts of South West Africa (Lawrence, 2),

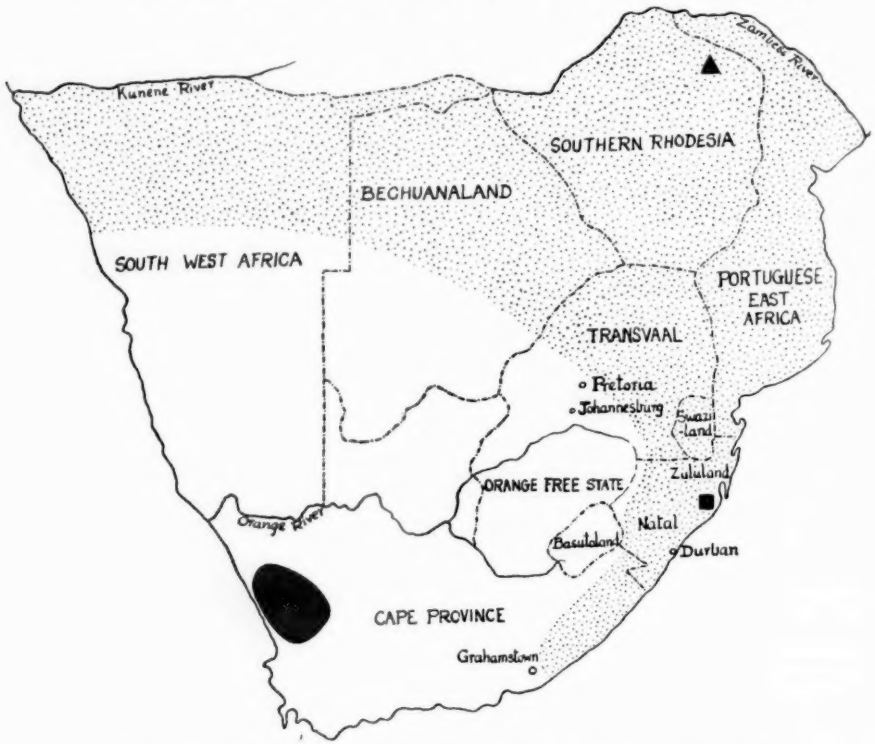

FIG. 1.—Distribution of the Pedipalpi in South Africa. Stippled area, *Damon variegatus* (Perty); black area, *Phrynichus scullyi* Purcell; ▲, *Phrynichus bacillifer* (Gerstaecker), based on a single specimen; ■, *Schizomus zuluanus* Lawrence, based on a single specimen.

and its geographical range is rather larger than indicated by Fage in his distribution map of the African Damoninae (6, p. 112).

Phrynichus scullyi Purcell.

P. scullyi Purcell, Ann. S. Afr. Mus., ii, pt. 6, p. 206, 1901.

The species was rather briefly described by Purcell and no illustrations were given of the type. The genus *Phrynichus* differs from *Damon* in

lacking a strong curved conical spine at the base of the dorsal surface of the hand and in not having the femur of leg IV biarticulate. As is mentioned by Purcell, *Phrynichus scullyi* agrees with *Damon* in possessing a basal spine on the hand, and in this respect it does not fall within the strict definition of the genus.

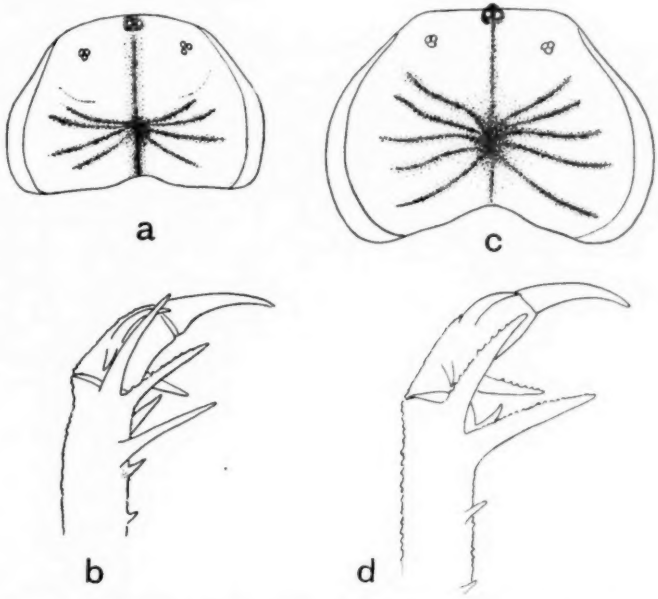

FIG. 2.—*Phrynichus scullyi*. *a*, carapace; *b*, dorsal distal apex of pedipalp. *Damon variegatus*. *c*, carapace; *d*, dorsal distal apex of pedipalp.

If the pedipalps of *Damon variegatus* and *Phrynichus scullyi* are compared it can at once be seen that there is a marked difference in the spination of the distal dorsal apex of the tibia of the two species, there being 2 long subequal spines in *Damon* and 3 long subequal spines in *Phrynichus*, as is shown in text-fig. 2, *b*, *d*. The most proximal of the three spines in *Phrynichus* is represented in *Damon* by a short spine hardly longer than the 3–5 spines which form a row along the anterior margin of the tibia. In juvenile, and sometimes also in half-grown specimens of *Damon variegatus*, this spine is not only relatively, but actually, longer than in the adults, and the group of 3 subequal spines of such young specimens closely resembles the condition found in adults of *Phrynichus scullyi*. In other words this lengthened spine, which is only a temporary and

adolescent feature of *Damon variegatus*, has become fixed and permanent in *Phrynichus scullyi*.

No mention is made of this clear-cut difference in the monographs of Kraepelen (7) and Werner (8); if such differences hold good in all species of *Damon* and *Phrynichus* they would doubtless have been used by authors to separate further these rather closely related genera. Two figures in Werner's monograph, which show the spination of the apex of the tibia in *Phrynichus* (figs. 17 and 179), are so different that they might well represent different genera. Purcell does not state what the relationships of *scullyi* are to other species of *Phrynichus*, but it seems to stand closest to *P. reniformis*. In the opinion of the writer, it represents a form more or less intermediate between *Phrynichus* and *Damon*.

The other differences between *Phrynichus scullyi* and *Damon variegatus* are slight, but the carapace of the former has a relatively greater width in proportion to its length as compared with the latter. The relation of the width of the carapace to its greatest length (measured at the side) is as 100 : 67 in *P. scullyi*, 100 : 74 in *D. variegatus*. All the known specimens of *P. scullyi* are distinctly smaller than the largest of *Damon variegatus*. The modified leaf-like hairs of the tarsi of the anterior legs, described below, are quite absent in *Phrynichus scullyi*, while always present in *Damon variegatus* of both sexes.

The Modified Structures and Sense-Organs of the First Pair of Legs in *Damon variegatus*.

Modified hair-like structures, apparently of a sensory nature, have been described on the first pair of legs by Hansen (4). Such hairs are found on the greatly elongated, flagelliform and multiarticulate tarsi of these appendages, appearing as in text-fig. 3, *a*. In spirit specimens which have been allowed to dry, in pinned Museum specimens, and in living animals they can be easily seen with the naked eye since they are white or cream-coloured, contrasting with the prevailing reddish brown of the tarsus itself. When examined under the microscope they are seen to be extremely delicate structures, the expanded portion of the hair being membranous and almost transparent, the main axis and chief rami, on the other hand, being stout and strongly chitinised. No modified hairs are found on any part of the tibia. On the tarsus they commence on the 8th to the 13th articulation, the first 3–5 hairs occurring on every second articulation and from then onwards fairly regularly at the junction of each articulation; the last 17–19 tarsal joints, which are distinctly shorter than the preceding ones, have no modified hairs of this type. The last 10 hairs of the series may be less regularly disposed on alternate articulations, as at the

beginning of the series. In the middle of the series the hairs may or may not be duplicated, occurring in pairs instead of singly and resembling a pair of small wings; the number of articulations in which the hairs are paired instead of single is variable.

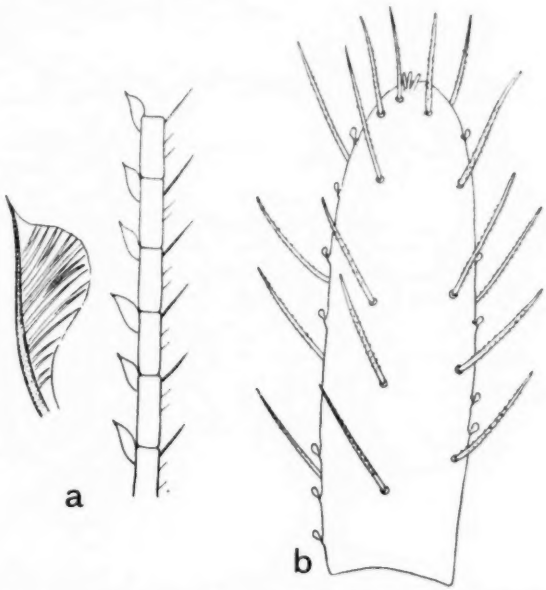

FIG. 3.—*Damon variegatus*. *a*, portion of tarsus of leg I, to show the modified leaf-like hairs, with one of these enlarged; *b*, apical segment of tarsus of leg I, showing sensory hairs and the normal spines of the segment, with a cluster of 3 sensory spines at the apex.

The Number of Hairs.—A series of specimens of *Damon variegatus* from Pietermaritzburg were examined in order to ascertain the number of hairs on the tarsi; these specimens were placed in the following categories: (*a*) full-grown adults (28–32 mm. in body length), 8 ♀♀, 12 ♂♂; (*b*) half-grown, *i.e.* fully chitinised specimens, but much smaller than the adults (12–18 mm.), 8 ♀♀, 8 ♂♂; (*c*) still smaller specimens (7·5–10·5 mm.) and with much lighter coloration than the half-grown specimens, 5.

In the adults the largest number of hairs counted in the females was 32, the smallest 18, in the males 28 and 12 respectively; the average number of hairs in both sexes was, however, the same, 24. In the half-grown animals the average number was much smaller, 12 in the case of the males and 11·5 in the females, the largest and smallest number being 17 and 9

respectively in the males, 15 and 9 in the females. In the group representing a still earlier stage the average was only 9, the number of hairs varying between 7 and 12.

From this it appears that the largest number of modified hairs in fully grown specimens is about 32, but if the duplication of hairs in the middle of the series is taken into account, the maximum would be in the region of 42, with an average of about 34 hairs. It also seems probable that they increase in number at each growth stage, the younger stages having progressively fewer hairs; none were found in any young pedipalps less than 7 mm. in body length, and they thus make their first appearance after the second or third moult, which is about the time the young leave the mother and commence an independent life of their own.

The hairs are firmly attached and cannot be readily loosened from the tarsus. Hansen considers them to have a sensory function, probably a tactile one. They appear to be found only in species of the genus *Damon*, though perhaps also in the remaining genera of the sub-family Damoninae, *Titanodamon*, *Musicodamon* and *Trichodamon*; as has already been stated, they do not occur on the corresponding segments of the first leg of *Phrynichus scullyi*.

Other sensory Structures of the Tarsi. — In *Damon variegatus* and *Phrynichus scullyi* other hair- or spine-like organs occur at the apex of the first tarsi; these seem to be sensory in function.

The extreme apex of the terminal segment of the tarsus, when examined under high power, shows a small group of 3 spines with their bases almost contiguous (text-figs. 3, *b*, 4, *b*); they appear to be hollow, and have a remarkable resemblance to the cone-shaped spines (*Sinneskegel*) at the apex of the last segment of the antenna in almost all Diplopoda; in these arthropoda they have been widely accepted as organs of olfactory sense. In the Diplopoda, with the exception of some of the Oniscomorpha, the number of these sensory cones is invariably 4, but in all the specimens of *Damon variegatus* and *Phrynichus scullyi* which I have examined the number is 3. In *P. scullyi* the spines have much the same general appearance as those of *Damon variegatus* (text-fig. 4, *b*).

A second type of sense organ found on the tarsus is considerably smaller than these apical cones or spines, which are themselves small; a number of these are found on each of the last 17–19 segments, only those seen in profile on the lateral margins of the last segment being shown in text-fig. 3, *b*. They are minute and rather rounded club-shaped hairs, which appear to have a circular opening distally, and a hollow interior containing structures which cannot be clearly seen in untreated material (text-fig. 4, *c*). These hairs begin on the segments where the large leaf-like modified hairs leave off, but may overlap them in a few segments; they

are thus found on the last 17–19 segments of the tarsus. In the proximal segments there are few of these hairs, the number increasing progressively towards the apex of the tarsus. In *Phrynichus scullyi* the same or very similar hairs are situated on approximately the same segments, viz. the last 15–17 tarsal articulations. Neither the apical spines nor the minute globular hairs are found on the tarsal segments of any of the remaining normal legs of these two species of pedipalps.

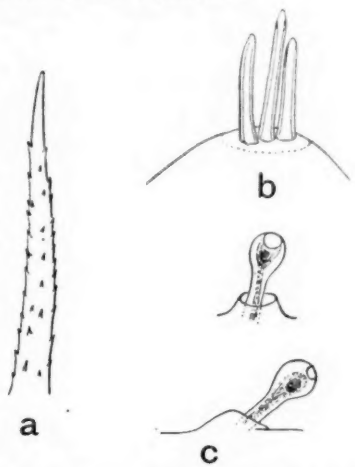

FIG. 4.—*Damon variegatus.* *a*, normal spiculated spine of the apical segment of tarsus I, enlarged; *b*, the cluster of sensory spines at apex of segment enlarged; *c*, globular sensory hairs found on the 17–19 terminal segments of tarsus I, enlarged.

OBSERVATIONS ON THE FUNCTION OF THE FIRST LEG IN *DAMON VARIEGATUS*.

As is well known, the anterior legs of the Amblypygous Whip-scorpions are very long and attenuated. In a full-grown specimen of *Damon variegatus* they may measure 25 cm. (10 inches) from tip to tip when both legs are extended well to the sides in the resting attitude, with an elbow bend at the junction of the tarsus and tibia; the tips of the tarsi may make slow questing movements. The leg is very supple, and by making use of all the joints the animal can rotate the whole appendage. Thus a specimen seated at the bottom of a cylindrical glass jar with a height of 5 inches can, without moving the body, raise the first leg vertically and explore the whole periphery of the rim of the jar with the tarsus. The tibia can be easily bent at the last 5 joints, which are more mobile than the rest of

the segment; the distal third of the tarsus is also more mobile than the proximal part of the segment and bending movements usually occur at these two places.

In confined areas, where a shorter length of organ is required, the distal third of the tarsus can be bent upon itself. The tarsus can turn and twist slowly in a curious manner, resembling the writhing of a tentacle rather than the more typical movements of the arthropod antenna. The extreme apex of the tarsus is used to touch the surface which is being explored, and this is done with tapping movements of extreme delicacy.

Secondary Sex Characters.

The secondary sex differences in the Amblypygi are, as stated by Werner and others, extremely small; in their general outward appearance there is

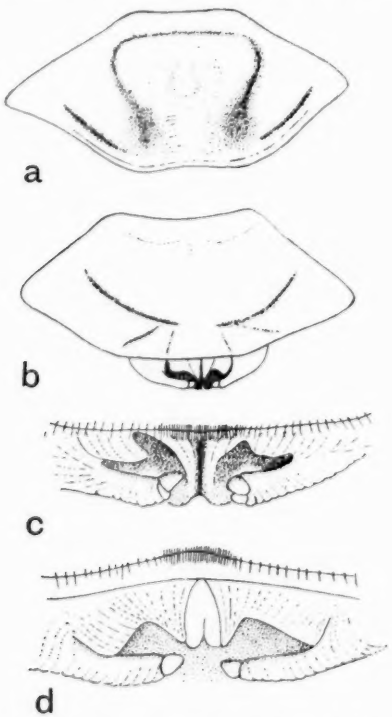

Fig. 5. — *Damon variegatus*. *a*, genital sternite of female; *b*, of male specimen; *c*. *d*, the sexual apparatus (enlarged) of two male specimens from Pietermaritzburg, Natal.

nothing to distinguish the males from the females except the shape and sculpture of the genital sternite. The differences of pattern produced by the grooves and depressions in this sternite, though not striking, are quite sufficient to enable the sexes to be distinguished with complete accuracy. In brief, that of the female (text-fig. 5, *a*) is characterised by two grooves which can be said to lie more or less longitudinally, though diverging somewhat anteriorly; they are generally united anteriorly by a transverse slightly curved groove. In the male, on the other hand, the grooves are on the whole transverse to the long axis of the body, though at the sides they curve somewhat forwards or towards the anterior end of the body; the grooves on each side thus diverge strongly from each other so that their anterior ends lie far apart and they are not joined by a transverse groove. In many males the paired papilliform penes protrude from beneath the posterior rim of the genital sternite, as can be seen in text-fig. 5, *b*, while text-fig. 5, *c*, *d*, represent the sex organs of two males from Pietermaritzburg under higher magnification. The whole of the male sexual apparatus shows no or very little chitinisation, although there are a number of characteristic grooves and folds, especially in connection with the gonopods themselves.

The Ventral Sacs.

In his admirable paper on African Pedipalpi (6) Dr. L. Fage gives figures of the ventral sacs on the third abdominal sternite of various Tarantulidae. According to him, the species in which they occur are *Musicodamon atlanteus*, *Titanodamon johnstoni* and *Damon diadema*. I can confirm his statement and that of Pocock (9) that these organs do not occur in *Damon variegatus*; in approximately 100 specimens which I have examined there is no sign of them, and they are thus found in only one of the three species of the genus *Damon*.

The Number of Eggs or Embryos in the Egg-sac.

Broods of 15 females of *Damon variegatus* were counted, 11 from various localities in Eastern Transvaal in the collections of the Transvaal Museum, and 4 from Natal (Natal Museum); the largest number of individuals (eggs or embryos) in a brood was 62, the smallest 17, the average per brood being 36. Three females from Pietermaritzburg carried 62, 58 and 48 embryos respectively, one from Estcourt, 33. The embryos from Estcourt were at an early stage, in which the rudiments of the newly formed appendages could be indistinctly seen through the covering membrane. In the female with a brood of 62 the embryos were at a late stage, with their covering membranes in process of being ruptured just previous to the

emergence of the embryos from the egg-sac; this stage resembled stage V described by Gough in *Admetus pumilio* (10), and was perhaps rather more advanced than Pereyaslawzewa's stage IV in *Phrynichus bacillifer* (11). All the appendages were well formed, the first pair of antenniform legs being much longer than the others and folded upon themselves; the position and relationships of the various appendages, when seen from the side and directly in front, are as in text-fig. 6. The greatest length of the eggs was found to be 3 mm., the greatest width 2·6 mm. Both eggs and embryos

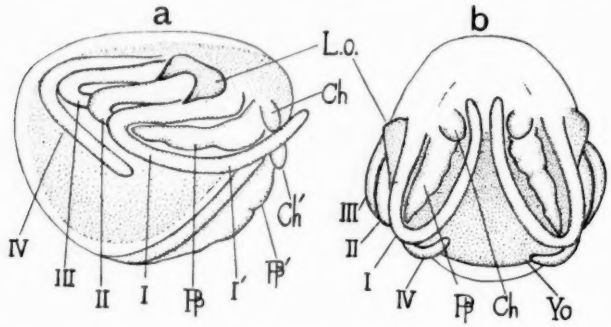

Fig. 6.—*Damon variegatus*. Late stage embryos taken from the egg-sac of a ♀ from Pietermaritzburg, Natal. *a*, from the side; *b*, from directly in front. L.o., lateral organ; Yo, yolk-sac; Pp and Pp′, right and left pedipalps, Ch and Ch′, right and left chelicerae. The legs denoted by Roman numerals.

are closely packed in the egg-sac, the pressure in the confined area giving a subangular outline to some of the contiguous eggs; the contents of the sac are not arranged in regular rows, either longitudinally or transversely, and are two layers deep throughout the extent of the sac.

Habitat.

The widespread *Damon variegatus* is a partly domesticated species, and it probably occurs in all buildings in Pietermaritzburg in the ventilation areas below floor-level. Specimens are also very common in outhouses, beneath stored furniture, packing-cases, and other large wooden structures which have been left undisturbed. In parks and gardens they often live under old tree-stumps or fallen trunks of trees. In more open country they are common under stones and in crevices of rocks; in indigenous forest under dried bark and under the fallen trunks of fairly large trees. There is little doubt that the species partly owes its wide distribution to the agency of man.

Nothing is known of the ecological background of *Phrynichus bacillifer*

and *Phrynichus scullyi*, but the latter is probably a rupicolous species; it seems to be considerably less common than *D. variegatus*.

It is not possible to state what the living conditions of *Schizomus zuluanus* are, but this single South African representative of the Uropygi probably lives in the humus of indigenous forests in Zululand; such a conclusion is based on the known habits of various Arachnids which were captured with it.

I wish to tender my sincere thanks for the co-operation and assistance rendered by the Directors of the various South African museums in placing their collections of Pedipalpi at my disposal. The distribution map representing text-fig. 1 is based on material loaned by the South African Museum (Dr. K. H. Barnard); the Transvaal Museum (Dr. V. FitzSimons); the Albany Museum, Grahamstown (Dr. John Hewitt); the Port Elizabeth Museum (Mr. J. A. Pringle); the McGregor Museum, Kimberley (Mr. J. H. Power); the National Museum of Southern Rhodesia, Bulawayo (Mr. R. N. Smithers).

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A NOTE ON THE VITRIFICATION OF KARROO SEDIMENT BY DOLERITE INTRUSIONS.

By J. J. Frankel.

(With one Text-figure.)

(Read September 21, 1949.)

Abstract.

New mineralogical and petrographical data obtained on three previously described occurrences of Karroo sedimentary material vitrified by dolerite are given. Where separable from the other constituents of the rock, the glass was chemically analysed; otherwise the composition was computed from a bulk chemical analysis.

Introduction.

Local vitrification of sediment by Karroo dolerite is on record from several localities in South Africa. Specimens from three of these localities were placed at the writer's disposal by Professor F. Walker and Dr. A. Poldervaart, during an investigation on intrusive glass in Karroo dolerite (Kent and Frankel, 1948). The field occurrences and microscopical features have been described previously, but the additional laboratory data since obtained on these specimens form the subject of this paper.

Other records of vitrification are from Stafelsberg's Vlei near Bird's river siding, C.P. (du Toit, 1905), and (on a very small scale) from Elandslaagte, Natal (Hatch, 1912). No further occurrences of fused sediment have been reported in South Africa more recently.

Vitrification of sediments by doleritic intrusion has been described in detail from many localities, including the Island of Soay (Harker, 1904) and Antrim (Reynolds, 1940; Tomkeieff, 1940). The glassy products bear an exceedingly close resemblance to those from South Africa.

Petrography.

(1) *Barkly East District, C.P.*—In 1904, du Toit described an occurrence of glassy material on the farm Coldbrook.

Two hand specimens from this locality, one a dark glassy rock and the other a medium-grained white quartzite, labelled "Coldbrook" and "Coldbrook sediment" respectively, were given to me.

du Toit records that an olivine-bearing dolerite sheet (of the Perdekloof type), 100 to 150 feet thick, is covered by a thin layer of Cave sandstone.

". . . The latter within a short distance from the dolerite has been vitrified and resembles a pitchstone in its black vitreous appearance. The vitrified rock passes insensibly into white quartzite and is often veined and streaked with quartz or else brecciated." "On this same ridge at Coldbrook there is a vein of black glassy rock in the dolerite much resembling a tachylite in appearance. It is well exposed near the top of the sheet and varies in thickness from six to eighteen inches."

Little can be added to the thin section description given by du Toit. Through the courtesy of the Director of the Union Geological Survey, I was enabled to examine du Toit's original sections of this occurrence. This examination has shown that slides of my hand specimen labelled "Coldbrook" resemble his slide 1213, *i.e.* the occurrence in vitrified Cave sandstone.

In thin section and under low-power examination the glassy rock is seen to consist of clear, pale brown glass in which are set rounded to subangular grains, predominantly quartz with a few of plagioclase, of sizes ranging from 10 to over 100 microns across and of average diameter 60 to 80 microns. These quartz grains are not uniformily distributed but tend to cluster in the glass. Under higher powers they appear subangular, oval or rounded, never angular. Most of the quartz grains are surrounded by a zone of lath-like crystals, generally with the longest dimension at right angles to the quartz boundaries and projecting into the glass (fig. 1, *a*). Individual laths have an average size of 1×10 microns. They have the same birefringence as, and are in optical continuity with, the quartz grains. They also occur as clusters, not necessarily surrounding quartz, in which all laths extinguish simultaneously under crossed nicols. It is considered that they are paramorphs of quartz after tridymite (*cf.* Reynolds, 1940). Tomkeieff (1940), in describing similar laths, has suggested that they might have been cristobalite.

Cordierite crystals, scattered throughout the glass, range from an average size of 5 microns square to 10×18 microns, and show cubic, rectangular and hexagonal outlines. They have a very low birefringence partly due to the thinness of the crystals in the sections, an approximate refractive index of 1·54, and make up 6 per cent. by volume of the rock.

A fair number of zircon grains, small black granules of magnetite, and a few cloudy patches which may be the last relicts of feldspar grains, are also scattered throughout the rock. Minute laths of a pale green mineral having

a small extinction angle may be an amphibole. High power also reveals small rounded spheroids, probably vesicles. There are no perlitic but only irregular cracks in the glass.

du Toit noted a considerable resemblance between the rock described above and the black glassy rock *in* the dolerite sheet on the same ridge. The pale brown glass contains a few quartz grains, all corroded and fringed

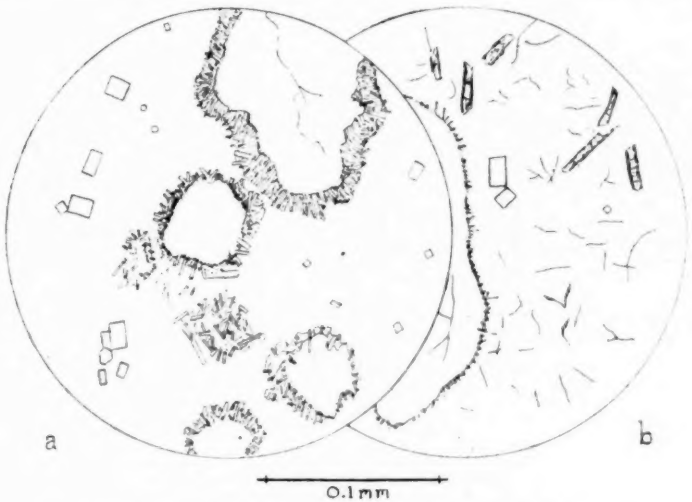

Fig. 1.—*a*. Camera-lucida drawing of a thin section of Coldbrook glassy rock showing equant, rectangular and hexagonal crystals of cordierite, and quartz grains surrounded by tridymite laths, set in glass.

b. Camera-lucida drawing of a thin section of fused Ecca grit from Heilbron showing equant cordierite crystals, laths of an unknown mineral of higher refringence, many crystallites, and a tridymite-fringed quartz grain set in colourless glass.

with tridymite; there is no cordierite. Perlitic cracks are quite distinct. du Toit did not consider that the field evidence available was sufficient to suggest that the two rocks were portions of the same fused sedimentary material.

It is quite possible that the sediment in contact with the upper margin of the dolerite sheet became sufficiently fluid and could penetrate the upper part of the dolerite itself. It may represent that portion of the liquid which had travelled farthest, and which carried few solid particles. The small amount of quartz present would support this view.

The specimen labelled "Coldbrook sediment" is a medium-grained grit. Under the microscope it is seen to be composed of grains of corroded quartz,

some plagioclase and relicts of another feldspar, presumably orthoclase. The grains average 0·3 mm. across, with the largest over 1 mm. in diameter, and are set in an isotropic, colourless glass which contains cloudy white or pale brown patches, possibly chalcedony. Some laths of secondary feldspar (?) are 8×160 microns in size, and have a small extinction angle. A few rectangular plates may be cordierite. The quartz is frequently bordered by a pale brown or cream-coloured anisotropic zone, which may have been tridymite now paramorphed by quartz or replaced by chalcedony. Zircon is not uncommon. It is suggested that this rock represents a stage in the vitrification of the Cave sandstone when most of the feldspar had been fused to glass but most of the quartz was still undissolved.

(2) *Heilbron District, O.F.S.*—Young (1918) recorded fused Ecca grits from two farms, Roodekraal and Cyfergat, in this district. All the relevant slides of the University of Cape Town Geological Department Collection were made available to me.

The hand specimen of the coarsest fused grit consists of a clear glass containing quartz and white opaque altered orthoclase and plagioclase grains all averaging 0·3 to 0·4 mm. in diameter. Under the microscope the colourless glass is charged with 1-micron-thick, hair-like crystallites (similar to trichites), and stouter needles (5×250 microns) of a mineral which has some resemblances to an amphibole. Cloudy or brown patches like opal around the quartz grains are abundant. Cordierite as rectangular plates, 18×9 microns in average dimensions, varies considerably in amount from slide to slide. It is very abundant in those slides of brownish glass—not unlike the Coldbrook material. An additional point of resemblance is the presence of fringes of tridymite around some of the quartz grains (fig. 1, *b*).

Specimens of the dolerite associated with these fused rocks are of coarse and fine varieties. The latter might well be termed a tholeiite. Lilac to brown patches of isotropic glass charged with many trichites and laths of the unknown mineral are interstitial to feldspar laths. This glass may be a mesostasis, but it might equally well be material introduced from the fused sediment—olivine is a fairly abundant constituent of this rock, and where it is in contact with the interstitial glass it shows no reaction borders. The coarse dolerite, by contrast, has only a little mesostasis, which does not owe its presence to the formation of the glassy rocks.

(3) *Mount Currie District, C.P.*—Glassy patches in a fine-grained tholeiite were recorded from Mount Arthur Peak by Poldervaart (1946). The tholeiite in thin section shows irregular patches of a glass which range from 5 mm. to less than 0·5 mm. across. The glass is pale cream to brown, not always clear, and is charged with an intricate network of minute needles of an unknown mineral, probably a pyroxene, which makes up about 10

per cent. of the glassy areas. Surrounding this glass proper is a thin brownish zone bordered by a narrow deeper lilac-brown glass also containing needles 2×60 microns in size. In this zone there are rounded patches of raspberry-like granules, probably pyroxene, clear rounded quartz grains, needles of the unknown mineral, of apatite, and a few zircon grains.

Chemical Analyses.

In order to obtain chemical data on the different glasses, the preparation of sufficiently pure samples of the glasses was of the utmost importance.

For the glass in the Mount Arthur tholeiite and in the coarse glassy grit from Heilbron, it was decided to hand-pick glassy fragments after a coarse crushing, and then to centrifuge these fractions, after a fine grinding, in bromoform of specific gravity from 2·4 to 2·5. By this method it was hoped to obtain reasonably pure glass. A check under the microscope showed finally that except for rare minute quartz particles the Heilbron glass was pure, but the Mount Arthur glass was contaminated by minute granules of pyroxene, fragments of iron ore, apatite and possibly some feldspar. The amount of material available was very small, and as no great improvement could be effected after repeated centrifuge treatment, this impure glass was used for the chemical analysis.

In the case of the Coldbrook material, it was decided to analyse a portion of the rock from which representative slides were also cut, so that the percentage of quartz could be determined micrometrically and the composition of the glass computed.

The result of the analyses are given in Table I.

For the calculation of the composition of the Coldbrook glass, the average value of quartz measured on five slides was taken. This was 13·2 per cent. by volume, or 14·52 per cent. by weight. Analysis 1*a* represents the composition of the glass fraction plus cordierite. If all the magnesia in the analysis is allocated to this mineral, it makes up about 4 per cent. of the rock. The removal of this amount of cordierite, using the theoretical formula, increases silica, for example, to 70 per cent., and brings the composition of the glass itself nearer that of the Heilbron glass (Analysis 2).

The chemical compositions as deduced from the refractive index and specific gravity composition curves of George (1924) show a fair agreement with the actual composition of Table I.

Although the specific gravity and refractive index of the Mount Arthur glass agree with those of the Coldbrook glass, the analysis is rather different, owing to the presence of so many impurities, but it is likely that its true composition is very similar to the other examples.

The similarity in chemical composition of these glasses is no doubt due

TABLE I.

	1.	1*a*.	2.	3.	1*b*.	2*a*.	3*a*.
SiO_2	74·16	69·72	72·57	64·28	72·95	76·67	68·50
TiO_2	0·41	0·48	0·18	0·48	0·50	0·19	0·51
Al_2O_3	12·66	14·80	13·08	14·12	15·50	13·81	15·05
Fe_2O_3	0·47	0·55	0·94	2·29	0·57	0·99	2·44
Cr_2O_3	n.f.	n.f.	n.f.	n.f.	..	..	..
FeO	1·16	1·36	0·50	2·81	1·41	0·53	3·00
MnO	0·11	0·13	0·02	0·04	0·13	0·02	0·04
MgO	0·34	0·40	0·08	1·34	0·05	0·09	1·43
CaO	1·21	1·42	1·12	3·96	1·48	1·18	4·22
BaO	0·04	0·05	0·08	0·07	0·05	0·09	0·08
Na_2O	3·31	3·87	3·75	2·33	4·05	3·97	2·49
K_2O	2·35	2·75	2·33	1·61	2·88	2·46	1·72
H_2O+	3·70	4·33	5·21	5·64	..	..	..
H_2O-	0·13	0·15	0·17	0·56	..	..	..
P_2O_5	0·18	0·21	0·23	0·49	0·22	0·24	0·52
	100·23	100·22	100·26	100·02	100·25	100·24	100·00
Specific Gravity	2·41	2·37 (calc.)	2·35	2·37			
Ref. Index Na Light ±·002	..	1·505	1·501	1·505			

1. Dark brown glassy rock, Coldbrook.
1*a*. Calculated composition of the glass fraction, Coldbrook (Analysis 1).
2. Glass separated from vitrified Ecca grit, Heilbron district.
3. Impure glass fraction separated from Mount Arthur Peak tholeiite.
1*b*, 2*a* and 3*a* are Analyses 1*a*, 2 and 3 respectively calculated to total water-free basis.
Analyst, J. J. Frankel.

to the essentially similar mineral composition of the source material. The proportion of the different feldspars must, however, have varied in each of the sediments, as Young has shown that a sample of the Heilbron glass contained about 7 per cent. of soda, while an amount of 3·75 per cent. was obtained in the present analysis. Plagioclase grains ranging from an albitic variety to labradorite do occur in all the sediments.

Poldervaart (1946) has shown that in some instances the distillation of volatiles, mainly water, from stoped sedimentary blocks has facilitated the formation of tholeiites from olivine-dolerites. The Mount Arthur occurrence of vitrified sedimentary material derived from stoped blocks and associated with tholeiite appears to support this theory. In the cases of vitrification here described, which are really of small magnitude, it is not very likely that any distillation of water from the sediments has altered the crystallisation trend of an olivine-dolerite intrusion.

The only slide available of the dolerite from Coldbrook is an olivine-bearing type, and although it contains patches of a green altered mesostasis,

it cannot be said that the rock is typically tholeiitic. Some of the igneous rock associated with the Heilbron occurrence appears to be tholeiitic; part of the interstitial glass may be due to an original crystallisation trend of the magma, and part to the action of "resurgent volatiles" (Poldervaart) derived from the sediment. This interstitial glass has a refractive index similar to that of the vitrified sediment.

The formation of tridymite indicates that the temperature of the intrusions was probably greater than 870 degrees Centigrade.

Thus the fusion of sediment may result in the formation of two types of glassy material: (1) a glass in the sediment, and (2) some glassy mesostasis in the igneous rock (resurgent volatile action). In addition, some glass may be introduced into the structure of the igneous rock from the first-mentioned type. This aspect of the problem requires further investigation, much of it in the field. The rather widespread vitrification of Ecca grits in the Heilbron district is at present under investigation by Mr. P. B. Ackermann; it is hoped that a clarification of such problems will result from his work.

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A MICA LAMPROPHYRE FROM MOORREESBURG, CAPE PROVINCE.

By Frederick Walker,
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(With one Text-figure.)

(Read March 16, 1949.)

Abstract.

A thin sill of mica lamprophyre intrusive into a thick limestone band in the Malmesbury series is described. The rock appears to be unique in the Western Province, and a chemical analysis shows it to have affinities with the kersantite group rather than the minettes.

Introduction.

During 1943 a visit was made by the author to a limestone quarry recently opened in the Malmesbury series about two miles S. 80° E. of Moorreesburg railway station. Amongst the rejected material on the quarry floor was a rock of unusual and striking appearance, which proved on microscopic examination to be a mica lamprophyre. At that time exposures of the lamprophyre on the working face were scanty, but subsequent visits in 1944 and 1946, when the quarry had been further developed by the Titan Lime Co., showed the intrusion to be a thin sill. At the time of writing, however, the old working face has been abandoned and is coated with mud, so that the lamprophyre can only be found now with great difficulty. Since the rock is apparently unique in the Western Province, a brief description seems merited.

The author desires to express grateful acknowledgment of data supplied by Dr. G. T. Lamont who visited the quarry in 1946, of the courtesy of the quarry staff, and of a grant from the Staff Research Fund of the University of Cape Town which defrayed the cost of a chemical analysis.

Field Relations.

Like the hornblende lamprophyre from Bellville, recently described by the author,* the Moorreesburg intrusion is concordant and of variable thickness. One or two isolated outcrops in the lower part of the quarry,

* F. Walker, "A Hornblende Lamprophyre from Bellville", Trans. Roy. Soc. S. Afr., vol. xxxii, pp. 189–194.

now being developed, may be downfaulted portions or dike-like offshoots. There can be no doubt, however, of the concordant nature of the main outcrop along the old working face where the lamprophyre in 1946 was seen to extend horizontally for 13 metres and to have a thickness of 2–2·5 metres. The limestone at this point dips approximately S.W. at 20°.

Petrography.

Megascopic.—The lamprophyre presents a striking appearance in the hand specimen, freshly fractured surfaces being spangled with countless flakes of black biotite up to 3 mm. across embedded in a dark grey matrix. Nevertheless, the rock is not easily distinguished from the surrounding dark grey limestone if at all weathered. The contact of limestone and lamprophyre appears neither knife-sharp nor truly gradational, this being probably due to thorough carbonation of the igneous margins. A few thin veins of calcite traverse the sill but ocelli are absent. The fracture of the lamprophyre is uneven and there is no trace of schistosity, but movement along prominent joint planes has given rise to slickensiding in places.

Microscopic.—The most prominent constituent of the rock in thin section is biotite, which makes up about 30 per cent. by volume of the rock. The dimensions of the flakes are seriate, ranging from 0·05 mm. to over 3 mm. in diameter. Most of the crystals are idiomorphic, particularly the larger ones, which tend to form glomeroporphyritic groups.

Many flakes have a dark, almost opaque, central portion surrounded by a lighter margin. This deepening in colour is seen under high powers to be due to minute rods of black mineral—probably rutile—occurring in parallel sets, closely packed and intersecting one another at about 60°. Apart from these rods the biotite is singularly free from inclusions.

The clear marginal portions of the biotite have the following optical properties:—

Refractive indices $\left\{\begin{array}{l}\gamma+\beta=1{\cdot}615\\ \alpha=1{\cdot}565\end{array}\right\}-0{\cdot}003$ $2V(-)=0°$ Pleochroism $\left\{\begin{array}{l}\beta,\ \gamma=\text{reddish brown}\\ \alpha=\text{pale yellow}\end{array}\right.$

Many of the smaller flakes show bleaching or alteration to greenish chlorite, but the larger ones are generally fresh.

The matrix of the lamprophyre is considerably altered, but appears to consist chiefly of kaolinized feldspar with subordinate amounts of quartz and secondary calcite. Some of the freshest feldspar shows traces of lamellar twinning, the extinction angles falling within the range of oligoclase, but it is possible that some potash feldspar is also present. The matrix is granular, with an average grain-size of 0·1 mm., but decomposition renders this figure somewhat doubtful. Not only are mica lamprophyres invariably

prone to alteration, but in the present case the sill has been penetrated by solutions circulating through the limestone country rock and has thereby been subjected to widespread carbonation. The marginal portions of the sill show no signs of chilling or change in texture, but the intense carbonation along the contacts would undoubtedly mask any such effect.

The chief accessory minerals of the lamprophyre are apatite (which is ubiquitous in the matrix as minute needles) and irregular scales of iron ore.

The limestone country rock, since it consists almost entirely of crystalline calcite, has suffered no significant contact metamorphism.

Chemical Analysis.

A typical specimen from the centre of the sill was analysed by Mr. F. Herdsman. The results are given below, together with other analyses for comparison.

Table of Analyses.

	I.	II.	III.
SiO_2	51·49	52·30	53·04
TiO_2	0·52	..	0·73
Al_2O_3	15·98	17·45	15·68
Fe_2O_3	0·95	1·80	4·25
FeO	5·76	4·80	4·41
MnO	0·28	..	..
MgO	6·12	8·50	5·79
CaO	6·19	4·78	6·02
Na_2O	2·13	2·12	3·28
K_2O	3·42	3·23	3·10
H_2O^+	3·72	3·70	2·49
H_2O^-	0·18		
P_2O_5	0·63	..	0·30
CO_2	2·40	2·40	0·88
	99·77	101·08	99·97

Norm of I.

Q	7·5
or	20·0
ab	17·8
an	12·0
C	4·5
hy en	5·3
hy fs	9·5
mt	1·4
il	0·9
ap	1·3
cc	5·5
H_2O	3·9
	99·6

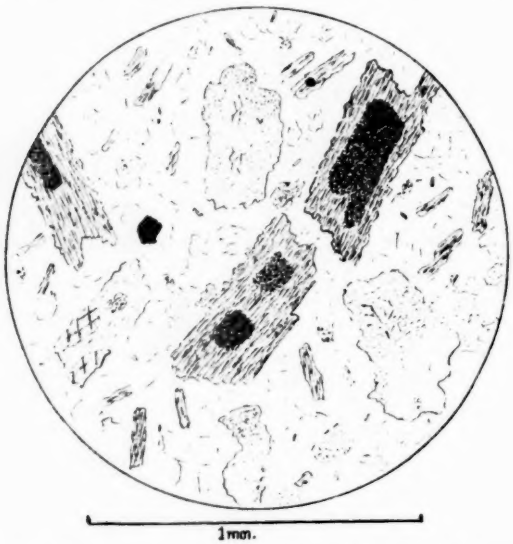
Specific gravity of I. = 2·80.

I. Mica lamprophyre, Titan Lime Co. Quarry, Moorreesburg, C.P. Analyst, F. Herdsman.

II. Kersantite, Hopital Camfront, Brittany. Analyst not stated. Quoted H.S. Washington, U.S. Geol. Survey, Prof. paper 99, 1917, p. 1045.

III. Average kersantite (54 analyses). Quoted from A. Johannsen, Petrography of the Igneous Rocks, vol. 4 (Chicago, 1937), p. 190.

The chemical composition of the Moorreesburg lamprophyre links it with the kersantite group rather than with the minettes, which invariably contain a higher percentage of K_2O. It agrees quite well both with a kersantite analysis of column II, of which the mode is given by Troeger,* and with the average of 54 kersantite analyses as calculated by Johannsen (column III).



TEXT-FIG.—Mica lamprophyre showing biotite flakes with dark centres and alteration to chlorite and calcite.

The relatively low K_2O percentage and the high CO_2 and H_2O figures are typical of this group.

AGE AND AFFINITIES.

The exact age of the Moorreesburg lamprophyre must remain in doubt. It is intrusive into the Malmesbury series, and has escaped the shearing movements which have had such a marked effect on the sedimentary rocks of the area. No comparable rock has been described from the neighbourhood, but the lamprophyre is probably a member of the suite of igneous rocks known to exist in the neighbourhood of Moorreesburg through the researches (as yet unpublished) of Mr. L. P. Rabie. Its affinities are definitely calc-alkaline, and it may well be a representation of a series of basic intrusions complementary to the silicic group associated with the

* W. E. Troeger, Spezielle Petrographie der Eruptivgesteine, Berlin, 1935.

granites of the S.W. Cape. Lamprophyric as well as silicic dikes have been described by van Biljon in association with the Kuboos pluton, though the single analysed kersantite is considerably more basic than the Moorreesburg example.*

* S. van Biljon, "The Kuboos Batholith, Namaqualand", Trans. Geol. Soc. S. Afr. vol. xlii, 1932, p. 193.

NAUPLIUS LONGISPINOSUS, A NEW LARVAL FORM OF BARNACLE.

By Eyvor E. Sandison, B.Sc., Honorary Research Assistant,
Department of Zoology, University of Cape Town.

(With four Text-figures.)

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Introduction.

The new nauplius described below was found in a plankton sample taken from the region of Swakopmund, S.W. Africa. The exact date and origin of this solitary sample cannot be traced, but it is known to have come from this area.

Dr. Gibbons, of the South African Division of Fisheries, while looking through some old plankton samples, discovered this strange nauplius, and later I obtained four others from the same haul. No cyprids were found.

The name *Nauplius longispinosus* has been given to these new larval forms, all of which appear to belong to the same species. Of the five specimens obtained one is younger than the others, the remaining four being of the same age. Assuming that the developing larva goes through six naupliar and one cyprid stage (Bassindale, 1936; Pyefinch, 1948), the youngest of these five nauplii would be placed in Stage II or Stage III (fig. 1, A), and the rest in Stage V or VI. No eyespots are visible, so this character cannot be used in assessing the age of the older individuals (Bassindale, 1936) with complete accuracy.

The younger stage of *N. longispinosus* resembles closely the younger larva of *Nauplius pelagicus* Rose, which Rose (1929) found in the plankton

off Algiers on 28th April 1926, and a comparison will later be made between these two species. Rose also described a more advanced stage of *N. pelagicus* found on 29th January 1927 which, although resembling the older form of *N. longispinosus* in some ways, shows such distinct differences that the two cannot be regarded as belonging to the same species.

The older stage of *N. longispinosus* resembles *N. eques*, which Chun obtained near Madeira in 1887 (Chun, 1896). Although both species are characterised by possessing a long dorsal spine, they can easily be distinguished by carapace measurements and by the very much longer abdominal process seen in *N. longispinosus*. Unfortunately, Chun does not give a full description of *N. eques* Chun, so a detailed comparison of setation formulae cannot be undertaken, but the differences mentioned above are considered sufficient to show that the two nauplii belong to two different species.

In the description of *N. longispinosus* which follows, Pyefinch's (1948) nomenclature for naupliar appendages and processes will be used throughout, and the setation formula according to Bassindale (1936).

Description of the Younger Stage.

This nauplius is estimated to be in Stage II or III.

The *carapace* measures 0·96 mm. in length (excluding fronto-lateral horns) and 0·6 mm. in breadth (fig. 1, B). The caudal spine is broken off at 2·28 mm., but the abdominal process is complete and measures 2·88 mm. Thus the complete nauplius is a grotesque animal with the abdominal process three times the length of the carapace and projecting down almost vertically from it. The carapace bears two elongated fronto-lateral horns directed forwards and downwards. Between the horns on the anterior edge of the carapace 2 small teeth arise on either side of a marked depression. There are 3 spines on the lateral margins of the carapace and 2 larger ones on the posterior margin. The first lateral spine is well in front of the middle of the carapace, the second is just behind the midline, and the third is half-way between the second and the two slightly projecting posterior carapace spines.

The *abdominal process* and *caudal spine* (fig. 1, C) are unusually elongated for a nauplius, and diverge at an angle of 35°–40°. The caudal spine is the stouter of the two, and possesses minute spinules projecting from it. On the abdominal process the minute spinules are slightly hooked with the points directed distally. These spinules are numerous at the proximal end but decrease gradually in number, though little in size, towards the distal end, leaving the tip free. About 0·8 mm. from the base of the abdominal process there arises a similar enlarged ventral spinule 0·16 mm. long.

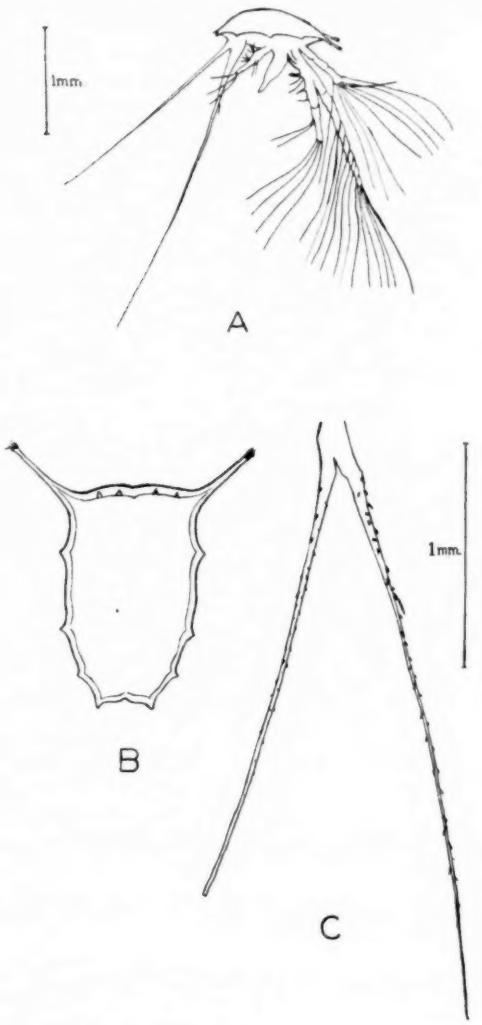

FIG. 1.—Young stage of *N. longispinosus.*

A. Lateral view.
B. Dorsal view of carapace.
C. Lateral view of abdominal process and caudal spine.

Cirriform appendages are not apparent within the abdominal process, nor are there any spinules to indicate their presence.

The *labrum* (fig. 2, A) is much elongated and projects prominently from the ventral surface. It is composed of a wider basal region leading to a

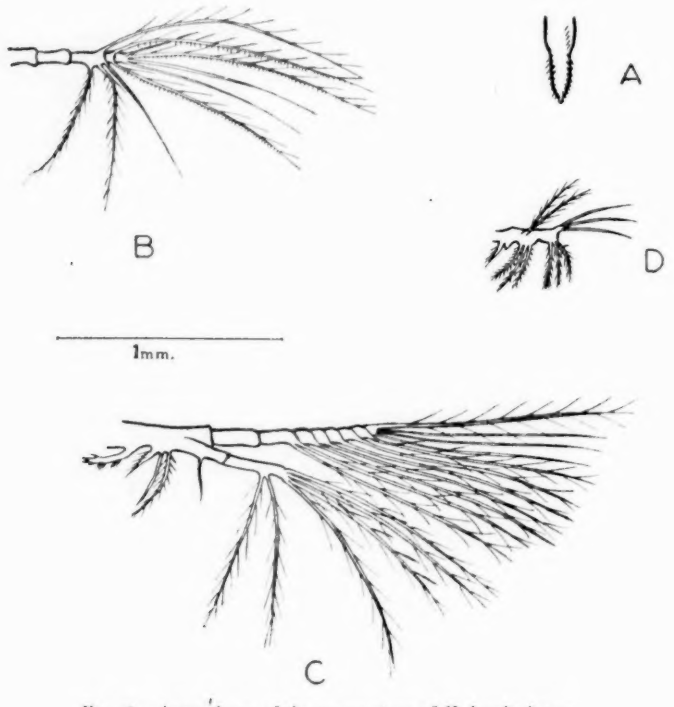

FIG. 2.—Appendages of the young stage of *N. longispinosus*.

A. Labrum.
B. Antennule.
C. Antenna.
D. Mandible.

definite "waist" in the mid-region, and the end tapers sharply to terminate in a button. Basally it bears a few short hairs, and from the "waist" 4 tracts of hairs run down the sides of the labrum to terminate in very fine minute spinules.

There are 3 pairs of appendages: antennules, antennae, and much reduced mandibles. The antennules and antennae measure 1·7 mm. and 2·4 mm. respectively from their bases to the ends of the setae.

Antennule (fig. 2, B): composed of 5 segments, the first two of which are without setae, the third bears 4, and the fourth and fifth segments are smaller in size and bear 2 and 4 setae respectively.

Setation formula: 1. 1. **4.** 1. 3.

1—long and plumose.
1—long and plumose.
4—1 long and plumose on one side and with short hairs on the other; 2 long and bare; 1 short and bare.
1—long and plumose on one side and with short hairs on the other.
3—2 long and plumose; 1 long and bare.

Antenna (fig. 2, C): composed of exopodite, endopodite and basipodite bearing a gnathobase. The whole appendage is long and slender, and the first segment of the endopodite has small teeth on its distal border.

Setation formula: 0. **2.** 9.—0. **4.** 2. 1. 3. G.

Exopodite:

0—(no setae on the anterior border of the exopodite).
2—1 long and plumose; 1 finer and without hairs.
9—2 fine and without hairs; 7 long and plumose.

Endopodite:

0—(no setae).
4—all long and plumose, with first seta slightly stronger than the rest.
2—long and plumose.
1—short, slender and bare.
3—1 short, bearing short hairs or setules; 1 short and bare; 1 short and strong, terminating in a spine with setules at its base.
G—curved towards the base of the appendage, and with two discs of setules on the convex surface near the end. Tip trifid, with a small curved spine on the concave surface.

Mandible (fig. 2, D): very much reduced, with a rudimentary exopodite of 2 segments.

Setation formula: 0. **2.** 0.—0. **3.** 3. 3. G.

Exopodite:

0—
2—short and slightly plumose.
0—

Endopodite:

0—
3—short, fine and devoid of hairs.
3—short and with setules.
3—short and with setules.
G—short, stout and curved, with short setules; a small pointed boss arises near the base.

This young nauplius possesses all the usual characters of a Cirripede nauplius, but the fronto-lateral horns, caudal spine and abdominal process, and setae on the antennules and antennae, are all very much elongated in comparison with those of the more common nauplii. It also differs from other nauplii in the possession of lateral carapace spines, spinules on the abdominal process and caudal spine, and teeth on the endopodite of the antenna. Spines on the labrum are not unusual, as during present investigations into the life-histories of the more common South African species of barnacle, the author has found spines on the labrum of larval *Chthamalus dentatus* (Krauss) and of *Octomeris angulosa* (Sow), but in *N. longispinosus* their position and character are distinct.

Description of the Older Stage.

This nauplius is estimated to be in Stage V or VI. The carapace measures 1·44 mm. in length (0·84 mm. excluding spines) and 1·26 mm. in breadth (0·84 mm. excluding spines) (fig. 3, A and B). The caudal spine is 9·1 mm. long and the abdominal process is broken off at 7·7 mm. The broken dorsal spine measures 6·0 mm.

The *carapace* (fig. 3, B and C) is longer than broad, with fronto-lateral horns projecting forwards and downwards, and each horn has a very small tooth at its base near the anterior border of the carapace. There are 3 short, stout spines on the lateral borders, and the posterior margin is enlarged into 2 prominent posterior carapace spines. The first lateral carapace spine is placed about one-third of the carapace length from the anterior end, and is separated from the second and largest carapace spine by two teeth. The second spine is situated just behind the middle of the carapace, and bears minute short hairs on it. The third spine is placed near the posterior end, and is separated from the second by two teeth and from the posterior carapace spine by one tooth. On the inner border near the base each posterior spine bears one tooth.

The long *dorsal spine* (fig. 3, C), projecting upwards and slightly backwards from the middle of the carapace, is the most distinctive feature of this naupliar stage. The middle of the carapace is raised to form a cushion

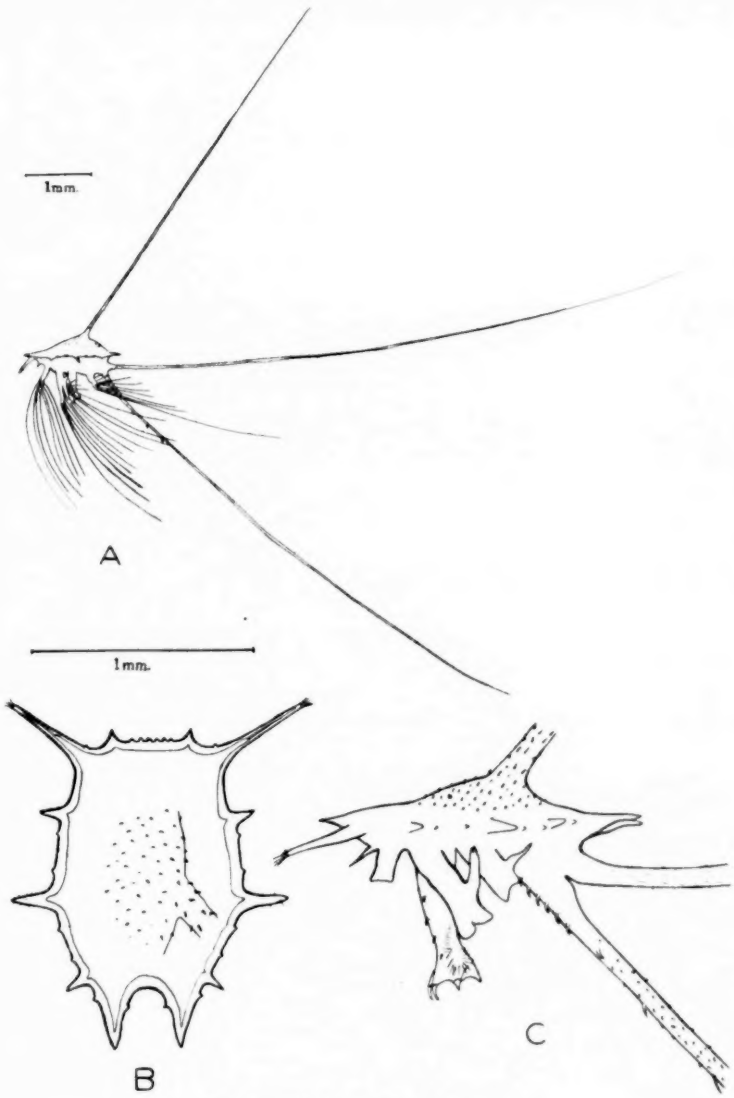

FIG. 3.—Old stage of *N. longispinosus.*

A. Lateral view.
B. Dorsal view of carapace.
C. Lateral view of carapace.

covered with minute spinules, which become larger at the base of the spine, but gradually diminish in size again and become fewer towards the tip.

The *abdominal process* contains 6 pairs of cirriform appendages within its base; the ends of these appendages project as strong curved hooks from the ventral surface. Below the cirriform hooks there are two more pairs of hooks placed a little distance apart down the process. The first pair is ventro-lateral in position, and the second pair are close together and ventral. Lower down on the ventral surface, about 1·4 mm. from the base of the spine, there is a single enlarged spinule corresponding to the one in the younger nauplius. Beyond these hooks and spinules the process is covered with minute curved spinules, which become smaller and fewer in number towards the tip.

The *caudal spine* is borne at an angle of 40°–45° to the abdominal process and is covered with minute spinules.

The *labrum* (fig. 4, A) is similar in shape to that of the younger stage, but the distal end is expanded and bears hooks. The short hairs on the basal and "waist" regions in the younger nauplius have been replaced by spinules in the older form, which has short hairs on the lower "waist" region and expanded distal end only. The distal end bears one pair of hooks anteriorly and another pair laterally, and fine hairs on the posterior border.

Of the appendages, the antennules and antennae have grown and now measure 2·4 mm. and 2·8 mm. respectively, and the mandibles have not only grown, but the exopodite is fully developed and bears one very long seta besides the normal shorter ones; this appendage now measures 2·9 mm. from its base to the end of the longest seta.

Antennule (fig. 4, B): composed of 6 segments; the second and third bear minute teeth on their distal borders, and all except the first bear setae.

Setation formula: 1. 1. **4**. 2. 4. 1.

1—long and plumose.
1—long and plumose.
4—1 strong and plumose on outer border, with short hairs on inner; 3 slightly plumose.
2—1 plumose on outer border and with short hairs on inner; 1 slightly plumose.
4—2 slightly plumose; 2 long, fine and bare.
1—thin and bare.

Antenna (fig. 4, C): exopodite and endopodite well developed. All segments of the exopodite bear small teeth along their distal borders.

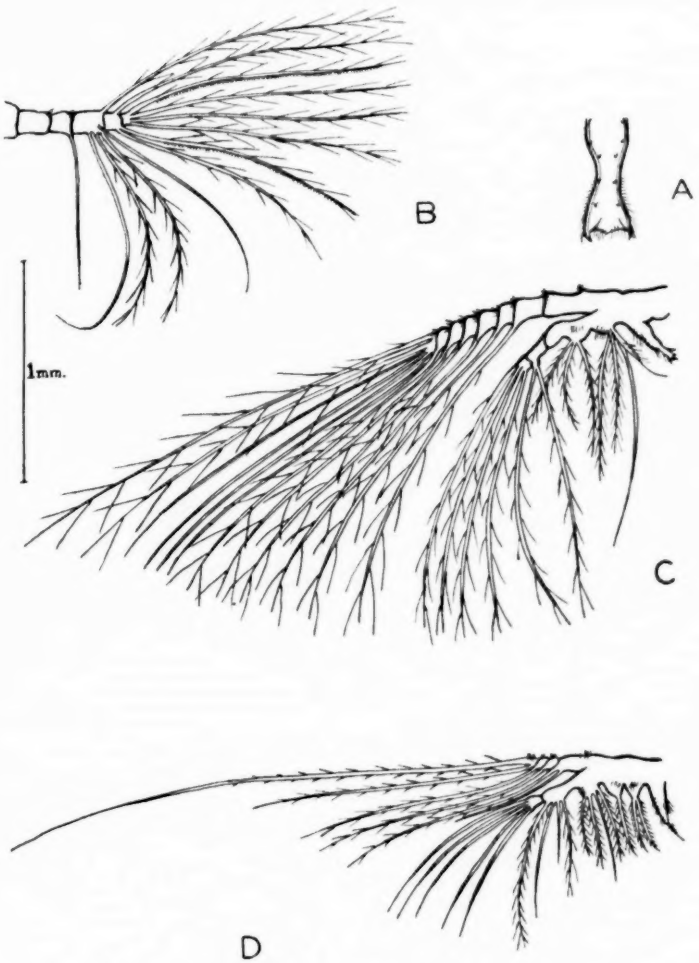

FIG. 4.—Appendages of the older stage of *N. longispinosus.*

A. Frontal view of labrum.
C. Antennule.
B. Antenna.
D. Mandible.

Setation formula: 0. **2.** 9.—0. **4.** 2. 3. 4. G.

Exopodite:

0—
2—long, strong setae with long plumose hairs.
9—first 4 long and bare; 5 densely plumose, especially towards tip.

Endopodite:

0—
4—long and densely plumose towards tip.
2—long and densely plumose towards tip.
3—1 medium length, 2 short; all possess setules.
4—1 long, thin and bare; 2 short with dense setules; 1 very short, thick and tapering at the tip to a seta with hairs at its base.
G—very short, strong and curved with 3 discs of setules on the convex surface; tip trifid, with a small spine on the convex surface and a larger one on the concave side.

Mandible (fig. 4, D): exopodite well developed, with small teeth on the distal border of each segment. Fine hairs arise from various parts of the appendage.

Setation formula: 0. **1.** 5.—0. **5.** 4. 4. 3. G.

Exopodite:

0—
1—very long, strong and slightly plumose.
5—4 long and slightly plumose; 1 shorter and bare.

Endopodite:

0—
5—fairly long and bare.
4—2 fairly long and slightly plumose; 2 short and bare.
4—3 short and densely setose; 1 short and bare.
3—short and densely setose.
G—very short, with a stout base tapering to a spine, which is curved towards the base of the appendage; base and bottom of spine hairy.

Discussion.

The two stages described above are obviously separated from each other by more than one metamorphosis in the larval life of the Cirripede. The older form is not only much larger, but it shows a marked advance in the development of appendages and in particular of the mandibles; also the cirriform appendages, which are not apparent in the younger stage, are well developed in the older. It is mainly the state of development of the

cirriform appendages which places the older form in Stage V or VI, as they are too well developed for a Stage IV nauplius. The younger stage possesses posterior carapace spines which characterise some Stage III naupliar species (Pyefinch, 1948) and are not seen in any Stage II, but as the carapace is unusually spinous in *N. longispinosus*, some hesitation is felt in placing this definitely in Stage III, as in this case these spines might have developed in an earlier stage.

Some conspicuous characters which are seen in their earlier stages in the young form are still present, and have become more fully developed, in the older nauplius. The three pairs of lateral spines in the young are larger and have become interspaced by teeth in the older form; the abdominal process after a few metamorphoses still possesses one enlarged spinule, and hairs on the labrum have been replaced by spinules. Comparing the setation formulae of the two stages, there is nothing to indicate that the older form might not have developed from the younger, as no setae are present in the earlier stage which are not represented in the later one. In the mandible of the older stage the setae are much more developed.

It is therefore possible to conclude that the two larval forms described above represent different stages in the larval development of the same species.

Comparison of *N. longispinosus* and *N. pelagicus* Rose.

The young stage of *N. longispinosus* resembles closely that of *N. pelagicus* obtained by Rose on 28th April 1926 off Algiers, but there are some outstanding differences:

(*a*) The carapace of *N. pelagicus* is 0·8–0·9 mm. long and has a curved anterior border, whereas that of *N. longispinosus* measures 0·96 mm. and the anterior border is straight.

(*b*) The abdominal process of *N. pelagicus* is approximately the same length as the carapace, while that of *N. longispinosus* is three times the carapace length. Both possess a single enlarged spinule about a quarter of the way down the process.

(*c*) The setation formulae are similar but there is one minor difference:

	Antennule.	Antenna.	Mandible.
N. pelagicus	1. 1. **4.** 2. 3.;	0. **2.** 9.—0. **4.** 2. 1. 3. G;	0. **2.** 0.—0. **3.** 3. 3. G.
N. longispinosus	1. 1. **4.** 1. 3.;	0. **2.** 9.—0. **4.** 2. 1. 3. G;	0. **2.** 0.—0. **3.** 3. 3. G.

The setation is identical in the antennae and mandibles, but the antennules of *N. pelagicus* possess one seta more than those of *N. longispinosus*. Bassindale (1936) found the setation formula to vary occasionally within the species, so that this character alone cannot be taken as diagnostic, but

in conjunction with the other characters mentioned above it confirms the theory that the young nauplius here described is different from *N. pelagicus*.

In the older nauplii the differences between the two species are even more marked:

(*a*) The carapace of Rose's *N. pelagicus* of 27th January 1927 measures 1·25 mm. long by 1 mm. broad without the spines, while that of *N. longispinosus* is 1·1 mm. long by 0·84 mm. broad.

(*b*) Dorsally the carapace of *N. pelagicus* supports a short spine and in front of this a spinous boss, but in *N. longispinosus* there is no separate boss, and a long, fine spine arises from the centre of a spinous cushion.

(*c*) Comparing the setation formulae:

	Antennule.	Antenna.	Mandible.
N. pelagicus	1. 1. **3.** 2. 3. 1.;	0. **2.** 9.—0. **4.** 2. 3. 4. G;	0. **1.** 3.—0. **5.** 4. 5. 3. G.
N. longispinosus	1. 1. **4.** 2. 4. 1.;	0. **2.** 9.—0. **4.** 2. 3. 4. G;	0. **1.** 3.—0. **5.** 4. 4. 3. G.

The mandible of *N. pelagicus* possesses one seta more than that of *N. longispinosus* and the antennule two setae less.

Because the dorsal spine of *N. pelagicus* is not so well developed as that of *N. longispinosus*, it might be suggested that *N. longispinosus* is an older stage of *N. pelagicus*; but this cannot be the case, as the carapace of the latter is longer that that of *N. longispinosus*, and *N. pelagicus* also possesses an extra seta on the mandible. It therefore seems likely that *N. longispinosus* and *N. pelagicus* are two different species, although they are undoubtedly closely allied.

Conclusion.

The two naupliar stages of *N. longispinosus* described above are almost certainly larval stages of sessile rather than of thoracic Cirripedes, and their spinous character, combined with well-developed swimming appendages, suggests a truly pelagic existence. It is possible, therefore, that they belong to the group of genera which become attached to the Cetacea, namely *Coronula*, *Tubicinella*, *Xenobalanus* and *Platylepas*.

Rose (1927) propounds the same theory that *N. pelagicus* may be the larval form of *Xenobalanus globicipitis* Steenstrup, found on the Cetacean *Globicephalus melas* Traill, or of *Platylepas bisexlobata* Blainv. which becomes attached to tortoises in the Mediterranean.

Darwin (1854) records several cases of species of *Coronula*, *Platylepas* and *Tubicinella* becoming attached to whales in the South Atlantic and around the Cape of Good Hope. It is therefore quite possible that *N. longispinosus* belongs to one of these genera.

Summary.

Nauplius longispinosus, a new larval form of Cirripede, is described.

Five specimens, representing two stages, were found in plankton samples from S.W. Africa. Both stages are described in detail, and the conclusion reached that they belong to the same species.

N. longispinosus is compared to *N. pelagicus* described by Rose, and the differences considered distinct enough to justify making the present form a new species.

In conclusion, the distinctive characters of *N. longispinosus* are summarised, and the theory is proposed that the adult barnacle belongs to the group which complete their life-history on Cetaceans, the nauplii being oceanic rather than neritic.

The author would like to express her grateful thanks to Professor J. H. O. Day and to Dr. N. A. H. Millard for their assistance in the preparation of this paper.

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METEOROLOGICAL OBSERVATIONS AT PIETERMARITZBURG, NATAL: RAINFALL INTENSITY AND ATMOMETRY.

By J. R. H. Coutts,* Department of Physics, University of Natal.

(Communicated by Dr. R. F. Lawrence.)

Meteorological observations have been maintained in the University grounds at Pietermaritzburg from 1938 onwards by Professor A. W. Bayer and the writer. For part of this period, the usual routine measurements have been supplemented by observations of rainfall intensities obtained with a Casella rainfall recorder, and of evaporation losses as measured with atmometers. The present note gives a summary of the results obtained from these observations.

Rainfall Data.

For the period 1938–1948, the annual rainfall aggregates vary between the extreme values 19·84 inches (in 1941) and 46·37 inches (in 1942), the mean value being 33·82 inches. From the figures shown under the headings "Sum" in Table I, it is seen that 89·8 per cent. of the precipitation occurred in the months September to April, and the remaining 10·2 per cent. in the winter months May to August; these results correspond fairly closely with those derived from the Meteorological Office Rainfall Normals (1939), where the figures 91·7 per cent. and 8·3 per cent. are quoted for a Pietermaritzburg station where the aggregates are considerably higher than those recorded in the University grounds.

Table I also gives an analysis of the rainfall intensity distribution. The intensities have been classified in five groups, as follows:—

> 2	.	Torrential rain.	Intensity exceeding 2 in./hr.
> 1	.	Very heavy rain.	Intensity between 2 in./hr. and 1 in./hr.
$> 0{\cdot}5$	.	Heavy rain.	Intensity between 1 in./hr. and 0·5 in./hr.
$> 0{\cdot}1$	.	Moderate rain.	Intensity between 0·5 in./hr. and 0·1 in./hr.
$< 0{\cdot}1$	.	Light rain.	Intensity less than 0·1 in./hr.

* The material presented in this paper formed part of a Thesis approved for the degree of Doctor of Science by the University of South Africa.

The analysis shows wide variations in the distribution for different periods. The annual proportions of very heavy *plus* torrential rains vary from 21 per cent. to 41 per cent. (the latter figure including a large proportion of the precipitation in a storm on 14th January 1947, when there was a fall of 7·28 inches in a few hours). The light rains always exceed 20 per cent. of the annual total, and amount to 38 per cent. in the drought year of 1941. For purposes of comparison with the distributions elsewhere in the Union of South Africa, reference may be made to Jackson's analysis (1934, 1935) of the rainfall at Johannesburg, and for the results reported (1943) for Bloemfontein. Jackson found no significant differences in the intensity distributions for the months October to March: averaging over twenty years, he found that in these months about 10 per cent. of the rain fell with intensity exceeding 0·5 in./hr., and that about 2 per cent. of the smaller precipitations from April to September belonged to the same group. Jackson's method of analysis under-estimates the intensities of short showers of high intensity, but his results show that the rainfall at Johannesburg contains a considerably greater proportion of moderate to light rain than is the case at Pietermaritzburg. On the other hand, the Pietermaritzburg results are in fairly close agreement with the data for Bloemfontein, where from 30 per cent. to 40 per cent. of the rain falls with intensity exceeding 0·5 in./hr.

The analysis of rainfall intensity, when combined with a consideration of rainfall aggregate over the same period, assists in making an estimate of the manner in which the rain-water is expended. The aggregate rainfall for the year gives an inadequate representation of the severity of a drought, such as that of 1941. In that year the total precipitation was 19·84 inches, but of this amount approximately 38 per cent. was made up of light rains and 34 per cent. of moderate rains. It has been shown (*e.g.* Coutts, 1945) that these low intensity rains, which are mainly made up of a large number of small precipitations of less than 0·1 inch, have a negligible effect upon the moisture status of the soil, and are thus largely wasted. At the other extreme, the torrential rains are partly lost by excessive run-off, and are liable to cause erosion, although these factors are less serious when the rain falls on ground with a good vegetative cover. As mentioned above, Jackson found no significant differences between the intensity distributions in the course of the summer at Johannesburg, but the data in Table I suggest that at Pietermaritzburg these storm precipitations are unusual in the earlier summer months (October and November), so that their erosive action is less severe than it would be if they occurred before the development of the summer growth. On the whole, it may be suggested that the most beneficial rains are those of heavy intensity, or of moderate intensity if they are of sufficient duration to give a total precipitation of about one-

T

Year.	1939 (aggregate 34·80″).						1940 (aggregate 36				
	>2	>1	>·5	>·1	<·1	Sum.	>2	>1	>·5	>·1	<
Jan.	1·6	5·2	0·8	1·3	5·3	14·2	0·5	3·6	2·4	1·8	3
Feb.	1·3	13·1	1·4	4·4	4.0	24·2	6·0	0·4	1·8	2·8	1
Mar.	..	0·1	2·1	2·3	1·8	6·3	2·9	1·5	1·0	3·3	1
Apr.	..	0·3	0·6	0·5	1·2	2·8	0·4	0·4	0·6	1·2	0
May	..	..	..	3·5	2·1	5·6	..	..	..	15·1	0
June	..	..	..	..	$0{\cdot}0_3$	0·0	..	..	..	3·1	4
July	..	..	..	1·2	0·6	1·8	..	..	..	0·4	0
Aug.	..	..	..	2·4	0·5	2·9	..	..	..	..	0
Sept.	..	0·6	1·4	4·4	2·4	8·8	..	1·1	1·5	0·7	1
Oct.	..	2·4	3·6	1·3	4·1	11·4	..	0·9	0·8	1·5	3
Nov.	..	0·2	2·1	3·6	5·8	11·7	0·8	1·4	0·5	5·5	4
Dec.	..	0·7	2·0	3·1	4·6	10·4	2·1	1·8	2·0	8·7	1
Totals	2·9	22·6	14·0	28·0	32·4	100·1	12·7	11·1	10·6	44·1	

* Aggregate for 11 months, January to November: 46·37″ for th

J. R. H. Coutts.

TABLE I.—RAINFALL SEASONAL DISTRIBUTION AND INTENSITY DISTRIBUTION.

(Percentages of annual aggregates.)

(aggregate 36·45″).				1941 (aggregate 19·84″).						1942 (aggregate* 37·89″).						1947 (aggregate 36·93				
>·5	>·1	<·1	Sum.	>2	>1	>·5	>·1	<·1	Sum.	>2	>1	>·5	>·1	<·1	Sum.	>2	>1	>·5	>·1	<·1
2·4	1·8	3·0	11·3	4·4	1·4	1·2	4·4	6·0	17·4	6·1	1·9	2·7	3·3	3·0	17·3	19·3	3·2	0·9	1·2	3·0
1·8	2·8	1·7	12·7	0·4	2·1	1·6	4·7	4·7	13·5	5·1	3·8	0·8	2·4	1·4	13·5	..	2·8	0·7	3·0	3·5
1·0	3·3	1·7	10·4	4·0	0·9	1·3	6·2	4·1	16·5	0·7	4·6	1·7	5·9	2·6	15·5	6·9	0·9	1·3	3·1	4·3
0·6	1·2	0·6	3·2	..	0·6	1·0	3·7	4·8	10·1	..	..	..	0·7	1·3	2·0	..	0·5	1·1	1·8	2·4
..	15·1	0·2	15·3	..	..	..	..	..	0·0	..	0·1	..	0·8	1·0	1·9	..	..	..	0·7	..
..	3·1	4·2	7·3	..	..	..	..	0·3	0·3	..	..	0·4	0·2	0·4	1·0	..	0·2	1·2	2·1	0·6
..	0·4	0·1	0·5	..	..	..	1·5	1·2	2·7	..	0·9	..	0·4	$0·0_4$	1·3	..	..	..	0·4	0·7
..	..	0·1	0·1	..	..	..	0·3	0·2	0·5	..	0·4	..	0·8	2·0	3·2	..	..	..	0·1	0·5
1·5	0·7	1·4	4·7	..	..	1·3	1·5	4·7	7·5	..	..	0·3	2·1	1·4	3·8	..	0·9	0·5	0·2	1·2
0·8	1·5	3·1	6.3	..	..	..	6·0	3·7	9·7	..	5·3	0·5	1·5	1·4	8·7	..	1·8	1·4	3·0	2·1
0·5	5·5	4·4	12·6	..	3·0	0·6	2·9	4·4	10·9	2·5	4·4	1·6	3·7	1·2	13·4	2·0	0·7	0·8	5·5	4·0
2·0	8·7	1·0	15·6	1·7	2·3	0·3	2·6	4·2	11·1	← no data →					[18·3]	1·3	0·3	0·5	3·4	4·1
10·6	44·1	21·5	100·0	10·5	10·3	7·3	33·8	38·3	100·2	[18·0] 14·7	[26·2] 21·4	[9·8] 8·0	[26·7] 21·8	[19·2] 15·7	99·9	29·5	11·3	8·4	24·5	26·4

er: 46·37″ for the year. In the totals for 1942, unbracketed figures are percentages of aggregate for the year, bracketed figures are per

L Distribution and Intensity Distribution.

ges of annual aggregates.)

19·84″).		1942 (aggregate* 37·89″).						1947 (aggregate 36·93″).						1948 (aggre		
<·1	Sum.	>2	>1	>·5	>·1	<·1	Sum.	>2	>1	>·5	>·1	<·1	Sum.	>2	>1	>·5
6·0	17·4	6·4	1·9	2·7	3·3	3·0	17·3	19·3	3·2	0·9	1·2	3·0	27·6	2·3	0·9	0·7
1·7	13·5	5·1	3·8	0·8	2·4	1·4	13·5	..	2·8	0·7	3·0	3·5	10·0	1·5	1·2	0·9
4·1	16·5	0·7	4·6	1·7	5·9	2·6	15·5	6·9	0·9	1·3	3·1	4·3	16·5	5·8	1·7	1·6
4·8	10·1	..	..	..	0·7	1·3	2·0	..	0·5	1·1	1·8	2·4	5·8	4·1	0·2	1·2
..	0·0	..	0·1	..	0·8	1·0	1·9	..	..	..	0·7	..	0·7	..	..	0·4
0·3	0·3	..	..	0·4	0·2	0·4	1·0	..	0·2	1·2	2·1	0·6	4·1	..	..	..
1·2	2·7	..	0·9	..	0·4	$0·0_4$	1·3	..	..	..	0·4	0·7	1·1	..	..	..
0·2	0·5	..	0·4	..	0·8	2·0	3·2	..	..	..	0·1	0·5	0·6	..	..	..
4·7	7·5	..	..	0·3	2·1	1·4	3·8	..	0·9	0·5	0·2	1·2	2·8	..	..	←
3·7	9·7	..	5·3	0·5	1·5	1·4	8·7	..	1·8	1·4	3·0	2·1	8·3	1·6	1·0	←
1·4	10·9	2·5	4·4	1·6	3·7	1·2	13·4	2·0	0·7	0·8	5·5	4·0	13·0	2·0	1·1	1·1
4·2	11·1	←		no data			→	[18·3]	1·3	0·3	0·5	3·4	4·1	9·6	8·2	4·7	2·0
38·3	100·2	[18·0] 14·7	[26·2] 21·4	[9·8] 8·0	[26·7] 21·8	[19·2] 15·7	99·9	29·5	11·3	8·4	24·5	26·4	100·1	25·5	10·8	

bracketed figures are percentages of aggregate for the year, bracketed figures are percentages of aggregate for

1948 (aggregate 32·72″).

·2	>1	>·5	>·1	<·1	Sum.
·3	0·9	0·7	4·6	4·8	13·3
·5	1·2	0·9	7·2	1·5	12·3
·8	1·7	1·6	4·2	3·9	17·2
·1	0·2	1·2	3·1	1·9	10·5
..	..	0·4	2·5	0·5	3·4
..	..	..	..	..	0·0
..	..	..	..	..	0·0
..	..	..	..	0·6	0·6
..	..	←——2·4——→			2·4
·6	1·0	←——6·8——→			9·4
2·0	1·1	1·1	2·5	3·8	10·5
3·2	4·7	2·0	2·3	3·1	20·3
25·5	10·8	63·6			99·9

f aggregate for 11 months.

to face page 316.

quarter inch; and the drought conditions of 1941 are more adequately represented when it is noted that the contribution made to the aggregate by heavy and moderate rains was 3·49 inches.

Atmometry.

The atmometer, as suggested by Livingston (1915), may be used to measure the "evaporating power" from a surface into the atmosphere; its chief advantage is the ease with which data may be collected, and its chief disadvantage lies in the difficulty experienced in determining the relative importance of the various factors which contribute to the observed loss in weight of the atmometer. These factors include the atmospheric temperature, the number of hours of sunshine, the humidity, cloudiness, wind velocity and direction, and the incidence of rain (Briggs and Shantz, 1917). Keen (1928) states that at Rothamsted the instruments were found to give useful data in rainless periods, and Haines (1925) found that with an instrument sheltered from the wind the readings were closely correlated with the hours of sunshine. In the following paragraphs we shall consider the extent to which the variance of the atmometer losses in weight can be accounted for by changes in atmospheric temperature and humidity; unfortunately, no quantitative data are available for wind velocity and hours of sunshine.

The routine observation of relative humidity at 08·30 hours gives a misleading idea of the humidity conditions in the local climate on account of the large diurnal variations (Bayer and Coutts, 1938), and atmometer losses have been correlated with humidity observations made at midday and with the maximum daily temperatures. Correlation coefficients have been calculated to show the relationships between the atmometer loss A and the variates P, H, and T, where P is the saturation pressure deficiency, H is the relative humidity, and T is the maximum temperature. It will be seen that the highest correlation coefficients are those connecting A and P. The values of r_{AH} and r_{AT} are slightly lower in all the longer periods shown at the foot of Table II, but these associations are not greatly reduced in the partial correlation coefficients $r_{AH \cdot T}$ and $r_{AT \cdot H}$, and are still highly significant. For the longer periods, $-r_{AH}$ is always slightly greater than $+r_{AT}$, but this is not the case in the monthly correlations, and it appears that, under local conditions, decreases in humidity and increases in temperature are of about equal importance in producing increased evaporation.

We can carry the analysis one step further by calculating the multiple correlation coefficients $(1 - R^2_{A \cdot TH})$, which give an estimate of the amount of variance in A that is not accounted for by the parameters T and H. The results for the longer periods included in Table II show that in three of the

TABLE II.—CORRELATION COEFFICIENTS BETWEEN A AND THE VARIATES P, H, AND T, DERIVED FROM OBSERVATIONS ON *n* DAYS.

Period.	*n*.	$+r_{AP}$	$-r_{AH}$	$+r_{AT}$	$-r_{AH\cdot T}$	$+r_{AT\cdot H}$	$(1-R^2_{A\cdot TH})$
Jan. 1939	29	·608	·565	·688	·270	·532	
1943	30	·818	·746	·714	·672	·628	
1944	31	·730	·725	·757	·404	·369	
Feb. 1939	26	·713	·612	·660	·464	·539	
1943	28	·851	·939	·713	·884	·172	
1944	28	·887	·823	·907	·228	·693	
Mar. 1939	26	·901	·903	·800	·749	·380	
1943	31	·568	·550	·730	·774	·885	
1944	30	·836	·872	·814	·690	·513	
Apr. 1939	27	·843	·461	·546	·665	·343	
1943	29	·842	·876	·881	·499	·526	
1944	30	·870	·931	·845	·815	·533	
May 1939	28	·872	·798	·801	·515	·525	
1943	28	·553	·570	·505	·456	·354	
1944	30	·486	·430	·457	·375	·408	
June 1939	30	·807	·669	·756	·391	·585	
1943	29	·808	·828	·715	·739	·544	
1944	30	·848	·913	·873	·661	·443	
July 1939	30	·844	·909	·758	·770	·036	
1943	29	·885	·906	·778	·836	·582	
1944	30	·726	·581	·679	·211	·472	
Aug. 1939	31	·871	·802	·869	·414	·658	
1943	30	·898	·923	·872	·725	·480	
1944	31	·773	·667	·791	·183	·591	
Sept. 1939	25	·953	·709	·734	·749	·636	
1943	29	·912	·905	·882	·704	·618	
1944	30	·886	·870	·822	·627	·435	
Oct. 1939	29	·785	·805	·854	·402	·596	
1941	28	·904	·522	·651	·878	·410	
1943	30	·572	·868	·922	·480	·730	
Nov. 1938	27	·933	·861	·731	·792	·572	
1941	28	·867	·645	·685	·610	·411	
1943	29	·838	·772	·785	·318	·381	
Dec. 1938	29	·850	·500	·522	·652	·567	
1941	30	·941	·731	·733	·581	·573	
1943	29	·527	·652	·373	·609	·237	
July 1938 to June 1939	333	·856 ± ·010	·712 ± ·018	·643 ± ·021	·713	·645	·288
Feb. 1941 to Jan. 1942	341	·684 ± ·019	·620 ± ·022	·604 ± ·023	·494	·469	·480
1943	351	·798 ± ·013	·698 ± ·019	·696 ± ·019	·636	·628	·311
Jan. 1944 to Sept. 1944	270	·797 ± ·015	·725 ± ·019	·672 ± ·023	·606	·565	·328

four cases about 70 per cent. of the variance is accounted for by the two parameters H and T, but that the proportion accounted for in this way in the drought year 1941 is very much smaller. The most probable explanation of the difference is that the wind velocities, as represented by Beaufort numbers, were greater in 1941 than in the other periods: in particular, the evaporation losses in the abnormally dry summer months from October to December 1941 were enhanced by unusually strong and persistent Berg winds.

Summary.

Meteorological data from Pietermaritzburg, Natal, yield the following results:—

(1) The annual rainfall varies between wide limits; about 90 per cent. of the rain falls in the months September to April. At least 60 per cent. of the precipitation falls with intensity exceeding 0·1 in./hr., and from 20 per cent. to 40 per cent. with intensities exceeding 1 in/hr.; the most intense precipitations occur between December and March.

(2) An examination of atmometer data indicates that up to 70 per cent. of the evaporation loss is determined by conditions of temperature and humidity; of the other contributory factors, wind velocity is probably the most important.

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SOME MARINE PLANKTON DIATOMS FROM THE WEST COAST OF SOUTH AFRICA.*

By Brian P. Boden, the Scripps Institution of Oceanography of the University of California, La Jolla, Cal., and Zoology Department, University of Cape Town, South Africa.

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(With 100 Text-figures.)

(Read November 19, 1947.)

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Preface.

I would like to express thanks to Professor J. Day, Zoology Department, University of Cape Town, for the financial assistance necessary in the preparation of this paper. Thanks are due also to Dr. Marston Sargent, and Dr. Martin W. Johnson, the Scripps Institution of Oceanography, University of California, and to Professor Wesley Coe, Osborn Zoology Laboratory, Yale University, for many valuable suggestions. I am especially indebted to Miss Elizabeth Kampa, the Scripps Institution of Oceanography, University of California, for her painstaking and laborious work in the correction of the manuscript.

Introduction.

The material upon which this report is based was drawn from the collection of the Division of Fisheries for the Union of South Africa for

* Contribution from the Scripps Institution of Oceanography, New Series, No. 451.

the years 1945–46, the collection of Dr. E. Roux of Vitamin Oil Co. Ltd. for the same period, some samples taken by Mr. J. T. Robinson of the Transvaal Museum, and some samples taken by me in the early part of 1945. All samples were taken in the area extending from a point just north of Lamberts Bay to a point just south of Cape Town. All were taken from the neritic province.

An endeavour has been made to list those species which apparently occur most frequently. However, reliable data on this point are lacking, due to the widely differing methods employed in collecting. Doubtless many species have been missed completely.

Numerous expeditions have occupied stations in this area before, but of these the "Valdivia" and "Discovery" are the only two, embodying full-scale diatom reports, which list the diatoms collected at each station. The South-West African species reported by Dr. Karsten of the "Valdivia" Expedition (68, 1905) and Dr. Hendy of the "Discovery" Expedition (62, 1937), but not found in the material reported upon herein, have, nevertheless, been included for the sake of completeness, and reference has been made to the source from which they were drawn. A search has been made through the literature for the clearest and most diagnostic figures of these species, and these have been borrowed freely, and reference made after each figure to the original author.

A general discussion of the structure, biology, and physiology of diatoms has been omitted as being outside the scope of this paper. However, most of the larger reports on diatoms contain discussions of this topic, and of these, Hustedt (1930), Lebour (1930) and Cupp (1943) are particularly good.

The classification followed herein is that of Schütt (1896), with modifications by Hustedt (1930–37). Attention is drawn also to the rather attractive classification propounded by Hendy (1937).

According to Sverdrup *et al.* (115, 1942, pp. 627, 628), in agreement with the dynamics of currents in the Southern Hemisphere, denser water of low temperature is found on the right-hand side of the Benguela current flowing up the west coast of South Africa. Under the influence of the prevailing winds surface layers are carried away from the coast and an upwelling of cold water occurs during most of the year. As a consequence of this upwelling, a band of water of low temperature is found along the coast extending to a distance of about two hundred kilometres, considerably wider than the continental shelf in this area (Shepard, F. P., 109, 1948). The presence of many warmer water forms such as *Fragilaria granulata* and *Stephanopyxis palmeriana* in the neritic province of this region would appear to be inconsistent with this. An examination of the surface currents as indicated by drift bottles, however (45, 1902, p. 155), reveals that

temporary currents occur which would be capable of carrying such forms from the warmer east coast. These forms probably appear more as guest-forms than as being typical of the plankton community of this area. On the other hand, these forms may lie dormant in localized regions throughout most of the year and appear periodically in the plankton in noticeable numbers in response to local warming. A much more intensive study of both east and west coast plankton is needed, and much more oceanographic data are required before the endemic plankton communities can be evaluated, and before it can be said with any degree of certainty that a particular species is present as a guest-form or as an endemic form. However, since the hydrographic conditions of the two areas differ so widely, it is highly probable that the east and west coast communities are fairly distinct in spite of very many common forms.

Methods.

All samples were preserved in formalin and sent to the Scripps Institution for examination. The plankton was washed in distilled water 5 or 6 times, allowed to settle for several hours and the supernatant water drawn off between washings. A hand centrifuge was used occasionally, but this tended to break up the more delicate chains.

Strewn plankton mounts were used throughout the investigation. Preliminary examination was carried out on plain water mounts. Frequently the best results were obtained from air-dried material mounted on a cover glass.

Hyrax, with a refractive index of 1·82, was the mountant used in preparing permanent mounts. The material was placed on a cover glass and either air-dried or very gently warmed. When dry, a drop of Hyrax was placed upon it and allowed to stand until the solvent had evaporated. The cover glass was then reversed and placed on a gently warmed slide. The cover glass could then have been sealed with lacquer or gold-size for more durable mounts.

For a detailed examination of the more robust and strongly silicified organisms the material was cleaned in acid. The plankton was boiled in concentrated hydrochloric acid, and concentrated nitric acid was carefully added to the boiling solution. When oxidation of the organic matter was complete (nitrous acid fumes ceased to be liberated) the frustules were allowed to settle and were well washed with distilled water.

Occasionally it was found desirable to flame some of the heavily silicified frustules to red-heat before mounting.

CLASSIFICATION OF THE CENTRICAE.

BACILLARIOPHYCEAE.

A. **CENTRICAE** Schütt.

I. **Discoideae** Schütt.

1. Coscinodisceae Schütt.

a. Melosirinae Schütt.
b. Skeletoneminae Schütt.
c. Coscinodiscinae Schütt.

2. Actinodisceae Schütt.

a. Actinoptychinae Schütt.
b. Asterolamprinae Schütt.

II. **Solenoideae** Schütt.

3. Solenieae Schütt.

a. Lauderiinae Schütt.
b. Rhizosoleniinae Schütt.

III. **Biddulphioideae** Schütt.

4. Chaetocereae Schütt.

5. Biddulphieae Schütt.

a. Eucampiinae Schütt.
b. Triceratiinae Schütt.
c. Biddulphiinae Schütt.
d. Hemiaulinae Schütt.

6. Eupodieae Schütt.

KEY TO THE CENTRICAE.*

A. Valves with a concentric or radiating sculpture around a point or points, central or lateral, never arranged in relation to a middle line. Without raphe or pseudoraphe. Outline circular, oval, or elliptical, sometimes polygonal, rarely crescent-shaped or spindle-shaped. Processes common . . . Section **CENTRICAE.**

I. Cells disc-shaped or cylindrical. Valves circular, their surface flat or convex, sometimes hemispherical. Valve sculpture arranged in relation to a central pole. Spines frequent. As a rule without horns or knobs; when present, small . . Subfamily **Discoideae.**

1. Valves circular. Not divided into definite sectors by ribs, rays, or undulating sectors. Sculpturing sometimes arranged in bundles. Knobs or eyes absent; more or less long spines often present . Tribe **Coscinodisceae.**

* Altered from Cupp (30, 1943, p. 34) to fit the Centricate genera of this region.

(*a*) Cells lens-shaped, round, or cylindrical. Usually united into more or less long typical chains. Intercalary bands often sculptured. Valve mantle usually strongly developed . . — Subtribe **Melosirinae.**
Genera: *Melosira.* *Stephanopyxis.*

(*b*) Cells short or elongated-cylindrical, bound into close chains by delicate siliceous projections or gelatinous threads. Cell wall usually weakly siliceous . — Subtribe **Skeletoneminae.**
Genera: *Skeletonema.* *Thalassiosira.*

(*c*) Cells disc- or drum-shaped, usually solitary, very seldom bound in chains. Valve surface slightly convex, rarely strongly convex, sometimes nearly flat or slightly concave. Intercalary bands hyaline or rarely very delicately sculptured. Valve mantle not particularly well developed . . . . — Subtribe **Coscinodiscinae.**
Genera: *Coscinodiscus.* *Planktoniella.* *Actinocyclus.*

2. Valves circular. Divided into distinct, complete or incomplete sectors by radial ribs or undulations or by wide hyaline rays from a characteristically constructed centrum. Without horns or prominent spines . . . . . — Tribe **Actinodisceae.**

(*a*) Valves divided into sharply distinct sectors by radial ridges uniformly running from the margin to the hyaline central area. Small but distinct spines usually at the marginal ends of these ridges. Alternate sectors generally depressed . . . — Subtribe **Actinoptychinae**
Genus: *Actinoptychus.*

(*b*) Valves sharply divided into sectors by broad hyaline rays running from a hyaline centre toward or to the margin, their outer ends marked with a minute spine: the hyaline centre divided into more or less wedge-shaped divisions confluent with the rays. Spaces between the radiating rays marked with fine, closely-set puncta arranged in radial or decussating rows . . Genus:	Subtribe **Asterolamprinae.** *Asteromphalus.*
II. Valves oval or circular in cross-section. Cells elongate, cylindrical or subcylindrical, with numerous intercalary bands, without internal septa. Valve structure arranged in relation to an excentric pole. Cells united into chains by their valves . .	Subfamily **Solenoideae.**
3. As above	Tribe **Solenieae.**
(*a*) Valves flat or raised, with or without marginal spines. Excentric process or asymmetrical spine absent . Genera:	Subtribe **Lauderiinae.** *Corethron.* *Schröderella.* *Leptocylindrus.*
(*b*) Valves with a single, often very short, spine or process, usually excentrically placed, thus destroying the symmetry of the cell. Valves flat or convex . Genera:	Subtribe **Rhizosoleniinae.** *Guinardia.* *Rhizosolenia.*
III. Cells box-shaped. Pervalvar axis generally shorter, sometimes slightly longer, than the valvar axis. Valves usually oval, sometimes polygonal, circular or semicircular; unipolar, bipolar, or multipolar, each pole represented by an angle or by a horn or spine, or by both angles and horns	Subfamily **Biddulphioideae.**
4. Valves with long setae, longer than the cells. Cells united into chains by basal part of the setae. Seldom living as single cells. Intercalary	

bands only seldom present. Valves circular or oval. All species pelagic
Genera:

Tribe **Chaetocereae.**
Bacteriastrum.
Chaetoceros.

5. Horns short and thick or, if longer, with claws at the ends. United into chains by the ends of the horns. Valvar plane circular or elliptical, usually with one to several poles. Valves, therefore, elliptical to circular, two- to many-angled. Intercalary bands and septa often present. Live partly in plankton, partly littoral. Majority of species marine. Colony building in chains frequent . .

Tribe **Biddulphieae.**

(i) Knobs and horns without claws on the end . .

(*a*) Valves bipolar. Cell wall weakly siliceous. Plankton forms . . .
Genera:

Subtribe **Eucampiinae.**
Eucampia.
Climacodium.
Streptotheca.

(*b*) Valves tripolar to multipolar, sometimes with bipolar varieties. Angles not bearing dome-like protrusions or horns. Intercalary bands frequently present. Marine forms, usually littoral, a few pelagic . .
Genus:

Subtribe **Triceratiinae.**
Ditylum.

(*c*) Valves bipolar, tripolar, or multipolar. Each angle with a dome-like protrusion or a horn. Usually strongly siliceous. Mostly large robust marine forms that build chains. Predominantly littoral, but sometimes pelagic. A few species are typically planktonic and are then more weakly siliceous . .
Genus:

Subtribe **Biddulphiinae.**
Biddulphia.

(ii) Horns with claws on the end.

(*d*) Valves bipolar, tripolar, or quadripolar. Each angle with a long vertical horn tipped with a claw; or in the bipolar forms either as described or having the angles of only one valve turned vertically upward into short-pointed ends without claws . . Subtribe **Hemiaulinae.**
Genus: *Hemiaulus.*

6. Cells without horns. Valves without internal septa. Valves semicircular, broader than long. Intercalary bands very seldom present. Cells in girdle view cuneate . . Tribe **Euodieae.**
Genus: *Hemidiscus.*

SYSTEMATIC ACCOUNT OF THE CENTRICAE.

A. **CENTRICAE.**

I. **Discoideae.**

1. COSCINODISCEAE.

a. Melosirinae Schütt.

Genera: I. *Melosira.*
II. *Stephanopyxis.*

Genus I. **MELOSIRA** Agardh (1, 1824).

Cells elliptical, circular or cylindrical, united in short chains by valve centres. Valves punctated. Intercalary bands none to numerous. Chromatophores numerous, small, plate-like. Nucleus central.

Species: *M. sphaerica.*

Species 1. **Melosira sphaerica** Karsten (68, 1905, p. 70).

Cells united in short chains. Valves circular, in girdle view cylindrical, with no definite sculpturing. Diameter 54–65 μ, length of pervalvar axis 60 μ. Chromatophores several small plate-like bodies.

This may not be a true *Melosira.*

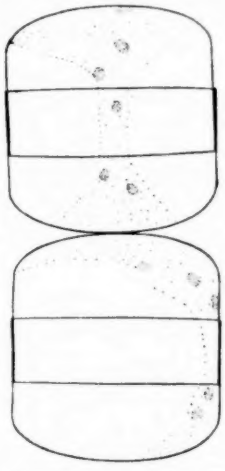

FIG. 1.—*Melosira sphaerica.* Diameter of cell 56 μ. Length of pervalvar axis 60 μ.

Genus II. **STEPHANOPYXIS** Ehrenberg
(37, 1844, p. 264).

Cells globoid or cylindrical with hemispherical valves. Form short chains with cytoplasm of adjacent cells in contact through stout, hollow spines situated on rounded ends and more or less parallel with pervalvar axis. Cell walls areolated. No intercalary bands. Small, round, numerous chromatophores. Resting spores noted.

Species: *S. turris.*
S. palmeriana.

Species 1. **Stephanopyxis turris** (Greville and Arnot) Ralfs
(99, 1861, p. 826).

Synonyms:

Creswellia turris Greville and Arnot (52, 1857, pl. xiv, p. 109), *Pyxidicula appendiculata* Ehrenberg (37, 1844, p. 85), *Stephanopyxis appendiculata* Ehrenberg (37, 1854, pl. 18, f. 4), *Creswellia turgida* Greville (53, 1859, p. 165), *Stephanopyxis cylindrica* Ehrenberg (37, 1873, p. 214), *Stephanopyxis niejahri* Ehrenberg (37, 1873, pl. 2, f. 1), *Stephanopyxis turgida* (Greville) Ralfs (99, 1861, p. 826).

Cells cylindrical with strongly convex valves. 10–28 spines at each end. Spines slightly thickened at tips, with a line of fusion midway

between neighbouring cells. Coarse hexagonal areolations all about the same size arranged in rows parallel with pervalvar axis or oblique to it.

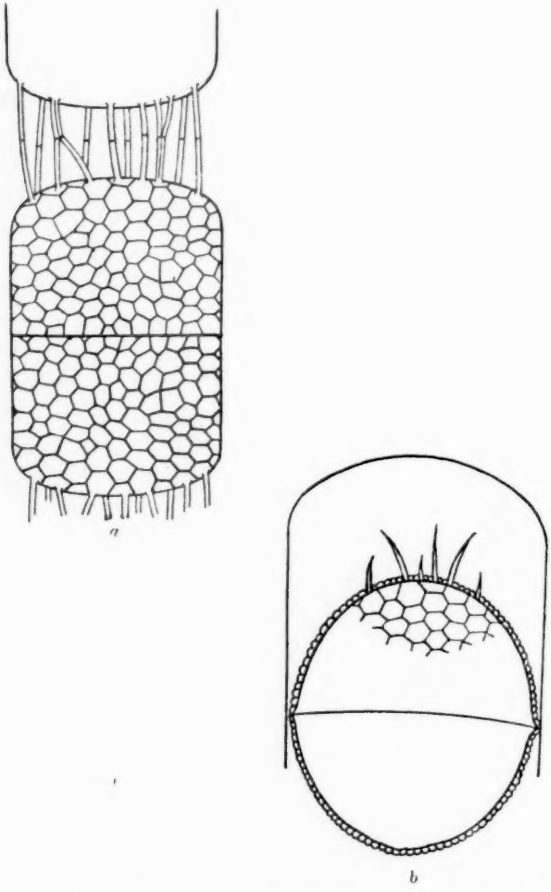

FIG. 2.—*Stephanopyxis turris*. *a*. Diameter of cell 42 μ. *b*. Resting spore.

About eight areolations in a row from valve margin to centre of cell in girdle view. Occasionally slightly constricted in valve mantle. Diameter of cell 36–57 μ. Resting spore with thick walls and strong spines.

A persistent form in the Cape West Coast Plankton has 12–14 equal areolations in a row from valve mantle to girdle zone. These are the same

size as the areolations in the type, viz. 3½–4 in 10 μ. The pervalvar axis of this plant is longer and the apical axis shorter than in the type. Both forms appear in the same sample with no intermediate forms. Karsten (68, 1905, pl. 2, f. 1) figures a *Stephanopyxis* from the Antarctic which he designates *S. turris*. This form has 14 apparently smaller areolations in

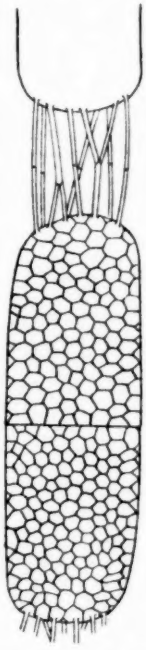

FIG. 3.—*Stephanopyxis turris*. Diameter of cell 36 μ.

a row from girdle band to valve mantle. Lebour (73, 1930, p. 73) considers that this form with the finer more numerous equal areolations constitutes a separate species. Greville (53, 1859*a*, p. 165) established a species *Creswellia turgida* on forms found in Californian guano, which had finer, more numerous equal areolations. This species, later designated *S. turgida* (Grev.) Ralfs (99, 1861, p. 826), has since been absorbed in the synonymy of *S. turris*.

Whether the form figured in fig. 3 is a separate species, as its presence in the same sample with the type would indicate, I hesitate to say. Karsten's figure may be of a form intermediate between the two which was not present in my material.

Species 2. **Stephanopyxis palmeriana** (Grev.) Grunow
(56, 1884, p. 38).

Synonyms: *Creswellia palmeriana* Greville (53, 1865*b*, p. 2).
Stephanopyxis campana Castracane (23, 1886, p. 88).

Cells cylindrical with rounded ends, similar in shape to *Stephanopyxis turris*. Form chains with cytoplasm of adjacent cells continuous through

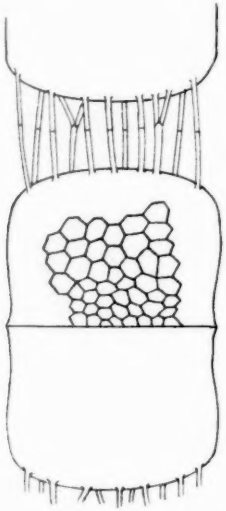

FIG. 4.—*Stephanopyxis palmeriana*. Diameter of cell 51 μ.

spines at ends of cells. Finer areolations than *S. turris*, and dwindling in size toward girdle line.

The constriction of the valve mantle is apparently of no specific significance. Cupp (30, 1943, p. 40) states that it is characteristic of *S. palmeriana*. Hendy (62, 1937, p. 237) quotes it as being characteristic of *S. turris*.

Many intermediate forms exist and the two species are easily confused, thus the distribution records are probably unreliable. The genus stands badly in need of revision and the literature is extremely confused.

b. Skeletoneminae Schütt.

Genera: I. *Skeletonema*.
II. *Thalassiosira*.

Genus I. **SKELETONEMA** Greville
(53, 1865*b*, p. 43).

Cells circular, cylindrical, or weakly spherical. Valves flat to strongly convex, without distinct sculpturing. Row of fine marginal spines parallel with longitudinal axis. The junction of these spines with those of the next cell unites the cells into chains. Cytoplasm of adjacent cells is in contact through these spines. Chromatophores one or two per cell. Nucleus central.

Species: *S. costatum.*

Species 1. **Skeletonema costatum** (Greville) Cleve
(24, 1878, p. 18).

Synonym: *Melosira costata* Greville (53, 1866, p. 66).

Cells circular, cylindrical, with rounded ends. Form long thin chains. Spines straight and slender. Space between cells usually longer than cells. Two chromatophores per cell. Nucleus central. Diameter of cell 3–16 μ.

Genus II. **THALASSIOSIRA** Cleve
(24, 1873*b*, p. 6).

Cells drum-shaped, united in flexible chains by a cytoplasmic thread. Occasionally solitary or embedded in an amorphous gelatinous mass. Valves flat, sometimes depressed in centre, delicately punctated. Marginal spinulae or spines present. Intercalary bands present. Numerous, small, plate-like chromatophores.

Species:

T. decipiens.	*T. subtilis.*
T. rotula.	*T. hyalina.*
T. condensata.	*T. excentrica.*

Key to Species.

A. One intercalary band.

B. Valve structure very delicate, almost invisible.

C. Striae punctate, very delicate, but arranged radially — *T. hyalina.*
D. Punctation delicate, but in no particular order . — *T. rotula.*

B_1. Valves noticeably meshed.

E. Marginal spinulae strongly curved, one apicule present . . . . . — *T. decipiens.*
F. Marginal spinulae short, apicule lacking . . — *T. excentrica.*

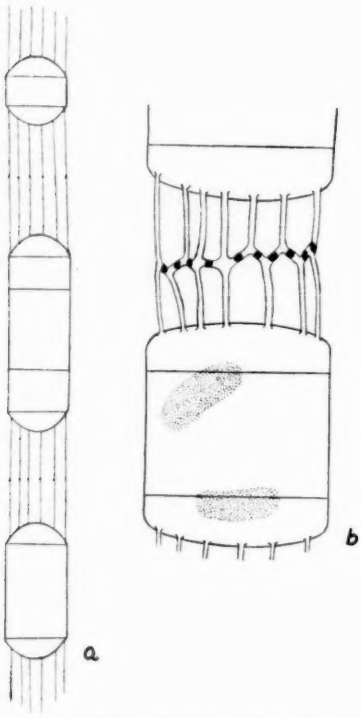

FIG. 5.—*Skeletonema costatum*. *a*. Part of chain, diameter 5 μ.
b. One cell, diameter 10·8 μ.

A_1. More than one intercalary band.

G. Colonies united in chains . . . . . *T. condensata.*
H. Colonies in gelatinous mass . . . . . *T. subtilis.*

Species 1. **Thalassiosira decipiens** (Grunow) Jörgensen
(67, 1905*c*, p. 96).

Synonyms:

Coscinodiscus excentricus Schmidt (103, 1874, pl. 3, f. 38), *C. excentricus* var.? *decipiens* Grunow (56, 1878, p. 125), *C. decipiens* Grunow (119, 1880, pl. 91, f. 10), *Thalassiosira gelatinosa* Hensen (63, 1887, p. 87), *C. excentricus* var. *gelatinosa* Cleve (24, 1897*a*, p. 23), *C. gelatinosus* Lemmerman (74, 1899, p. 266).

Cells drum-shaped, united in loose chains by cytoplasmic threads

30–80 μ in length. Occasionally in gelatinous irregular colonies. Valves slightly curved, with row of strong curved spines and one apicule. Sculpturing similar to *Coscinodiscus excentricus*. Diameter 12–40 μ. Numerous small chromatophores. One intercalary band per valve.

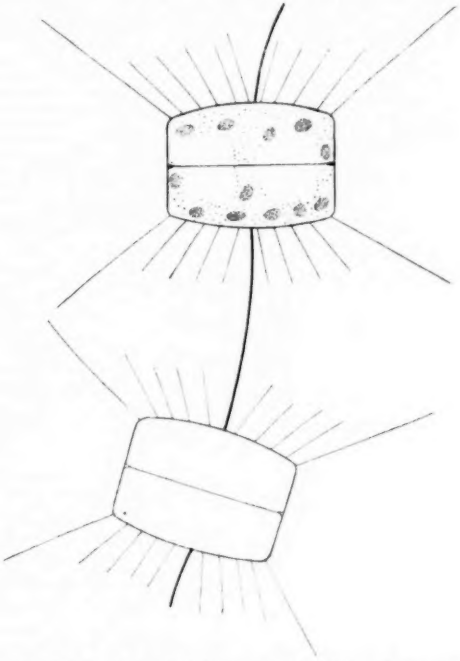

FIG. 6.—*Thalassiosira decipiens*. Part of chain, diameter 24 μ.

Species 2. **Thalassiosira rotula** Meunier
(84, 1910, p. 264).

Cells disc-shaped, united in chains by thick thread. Valves flat, rounded at margin. Delicate, regular punctation in no particular order. One unevenly thickened intercalary band per valve. Nucleus central. Numerous, small chromatophores. Diameter of cell 30–61 μ.

Species 3. **Thalassiosira condensata** Cleve
(24, 1900*a*, p. 22).

Cells somewhat rectangular in girdle view, valves circular, slightly depressed centrally, with single row of spinulae (sometimes with long

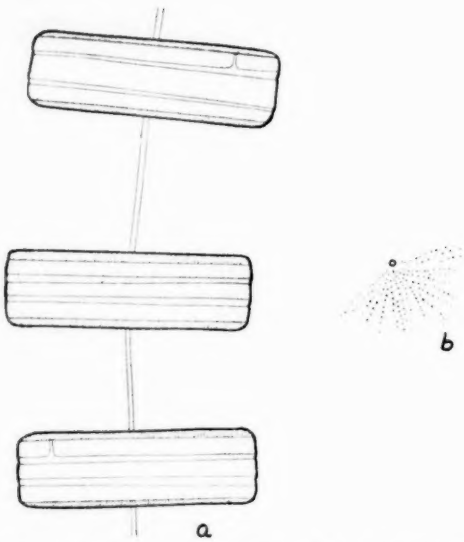

FIG. 7.—*Thalassiosira rotula*. *a*. Part of chain, diameter 42 μ.
b. Radiate punctation at valve centre.

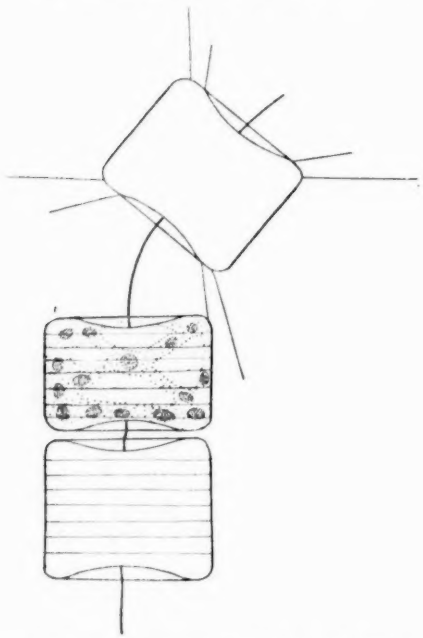

FIG. 8.—*Thalassiosira condensata*. Part of chain, diameter 31 μ.

radiating mucilage threads) directed obliquely outward. No visible sculpturing. United in chains by mucous thread. Numerous intercalary bands. Chromatophores numerous and plate-like. Diameter of cell 28–35 μ. Pervalvar axis 20–33 μ.

Species 4. **Thalassiosira subtilis** (Ostenfeld) Gran (47, 1900*b*, p. 117).

Synonyms:

Podosira subtilis Ostenfeld (93, 1899, p. 35), *Cyclosira bergoni* Péragallo (97, 1897, p. 438).

Cells drum-shaped or box-like, embedded in a gelatinous mass. Numerous intercalary bands. Valves rounded with no distinct sculpture. Diameter of cell 16–32 μ.

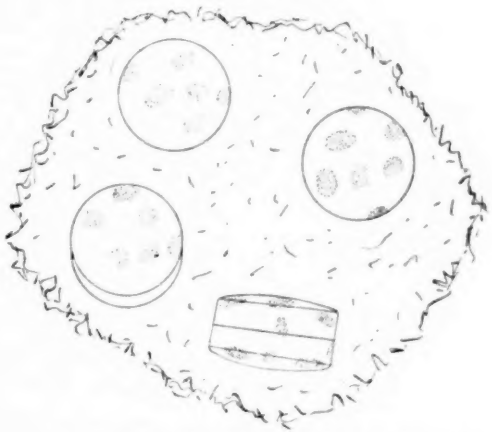

Fig. 9.—*Thalassiosira subtilis.* Part of colony, diameter of cells 18 μ.

Species 5. **Thalassiosira hyalina** (Grunow) Gran (47, 1897*b*, p. 4).

Synonyms:

Coscinodiscus hyalinus Grunow (56, 1880, p. 113), *Thalassiosira clevei* Gran (47, 1897*a*, p. 29).

Cells discoid, united in chains by central mucous thread. Valves flat, somewhat rounded at edges, furnished with radial striae, single apicule, and single row of small spinulae at margin. Diameter 24–48 μ, pervalvar axis about 10 μ. Chromatophores 8–10 small plates.

Neritic. Reported as unusual off South African coast by Hendy.

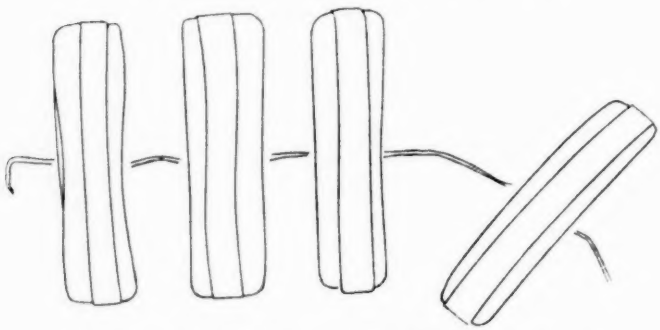

FIG. 10.—*Thalassiosira hyalina.* After Wilson in Lebour, 1930.

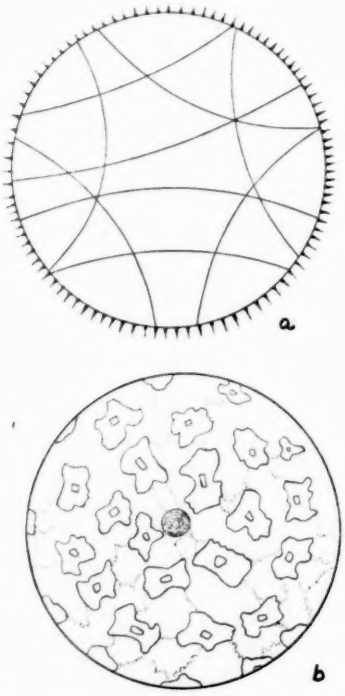

FIG. 11.—*Thalassiosira excentrica.* *a.* Valve view showing mesh plan. *b.* Valve view showing cell contents. Altered from Karsten, 1905.

Species 6. **Thalassiosira excentrica** Karsten
(68, 1905, p. 73).

Cells discoid, united in chains by central mucous thread. Valve structure precisely the same as that of *Coscinodiscus excentricus*, furnished with short but fairly well-pronounced marginal spinulae. Diameter 34–40 μ. Chromatophores proportionally large, biscuit-formed, with a single pyrenoid. A series of cytoplasmic bands connects the chromatophores with each other and with the nucleus.

Reported as numerous in the phytoplankton by Karsten.

c. Coscinodiscinae Schütt.
Genera: I. *Coscinodiscus.*
II. *Planktoniella.*
III. *Actinocyclus.*

Genus I. **COSCINODISCUS** Ehrenberg
(37, 1838, p. 128).

Pill-box cells usually single. Valves circular, finely punctated or hexagonally areolated and lacking large knobs or processes. In some species the areolations are more or less rounded and do not touch one another. Small marginal spinulae present or absent. Small apiculae (1 or 2) present or absent. If two are present they are asymmetrically situated. The central area of the valve may be smooth, sculptured, or with large areolae forming a rosette. Girdle is a single band to each valve. Intercalary bands often present. Numerous, small, plate-like chromatophores. Nucleus suspended in centre of cell by protoplasmic threads.

The genus has been divided into various groups by different authors, according to valve sculpture. Five main groups are represented here.

KEY TO SPECIES.

Group 1. **Inordinati.** Valves with delicately, radially striated margins; otherwise, however, punctation is irregular . . . *C. parvulus.*

Group 2. **Excentrici.** Valves flat or nearly so. Strongly hexagonally areolated. Areolations diminish in size from centre to periphery. Meshes curved and do not radiate from centre . *C. excentricus.*

Group 3. **Lineati.** Valves usually flat. Hexagonally areolated. Areolations diminish slightly in size from centre to periphery. Meshes straight in tangential lines based upon six sectors. Spinulae or apiculi present or absent . . . . *C. lineatus.*

Group 4. **Radiati.** Valves almost flat, convex or concave. Meshes radiate from centre but not in sectors. Tendency to dichotomy. Central rosette present or absent. Spinulae or apiculi present or absent.

A. Valves flat, cells discoid.
B. Central area or rosette lacking . . . *C. radiatus.*
B_1. Central area or rosette present.
C. Areolations equal in size . . . *C. janischii.*
D. Areolations increase in size toward periphery . . . . . *C. gigas.*
A_1. Valves arched or concave.
E. Valves convex, cells cuneiform in girdle view *C. granii.*
E_1. Valves convex, cells symmetrical in girdle view
F. Valve convex, centre slightly concave *C. rotundus.*
G. Valves uniformly convex . . *C. varians.*

Group 5. **Fasciculati.** Valves almost flat or slightly convex. Meshes radiate from centre in curved or straight radial sectors. Central rosette present or absent. Spinulae or apiculi present or absent.
A. Central area present, spinulae lacking . . . *C. curvatulus.*
B. Central area lacking, spinulae present . . . *C. subtilis.*

Group I. Inordinati.

Species I. **Coscinodiscus parvulus** Karsten
(68, 1905, p. 151).

Valves arched, with small "pearl-shaped" puncta scattered irregularly all over. Diameter 30 μ. Chromatophores small cocciform bodies.

Reported from this area by Karsten.

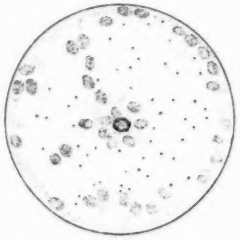

Fig. 12.—*Coscinodiscus parvulus.* Valve view. After Karsten, 1905.

Group 2. Excentrici.

Species 2. **Coscinodiscus excentricus** Ehrenberg
(37, 1839, p. 146).

Synonyms:

Odontodiscus excentricus Ehrenberg (37, 1846, p. 79), *Coscinodiscus labyrinthus* Roper (102, 1858, p. 21), *Coscinodiscus minor* A. Schmidt (103,

1875, pl. 113, f. 9), *Thalassiosira excentrica* Cleve (24, 1903*b*, p. 216), *Coscinodiscus heliozoides* Siddal (111, 1912, p. 377).

Cells discoid, 50–90 μ in diameter. Valves flat. Hexagonally areolated. Central areola has seven areolae grouped around it. Areolae bigger near the centre than near the margins. Meshes curved and not radiating from the centre. Spinulae arranged in irregular circle.

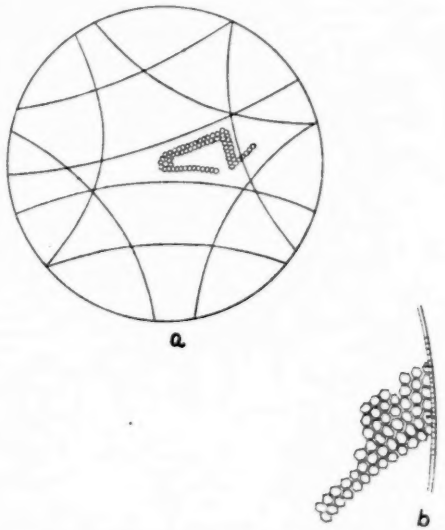

Fig. 13.—*Coscinodiscus excentricus.* *a.* Mesh plan, diameter of cell 59 μ. *b.* Areolation at margin.

Group 3. Lineati.

Species 3. **Coscinodiscus lineatus** Ehrenberg

(37, 1838, p. 129).

Synonyms:

Coscinodiscus ehrenbergi O'Meara (92, 1875, p. 264), *Coscinodiscus macraeanus* Grunow (103, 1875, pl. 59, f. 26), *Coscinodiscus lineatus* var. A. Schmidt (103, 1875, pl. 59, f. 31), *Coscinodiscus leptopus* Grunow (119, 1880, pl. 131, f. 5), *Coscinodiscus* spec. A. Schmidt (103, 1875, pl. 114, f. 13).

Cells discoid, 35–60 μ in diameter. Valves flat, hexagonally areolated. Areolae smaller near periphery than near the centre. Circular apertures

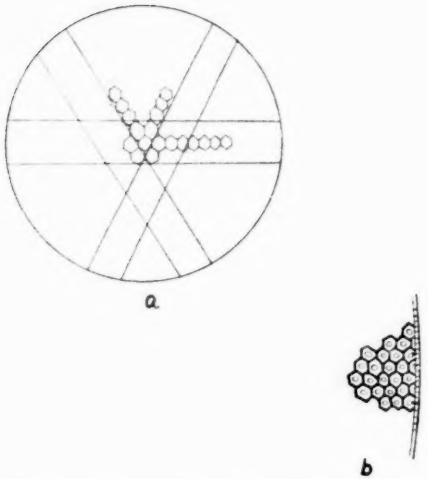

FIG. 14.—*Coscinodiscus lineatus*. *a*. Mesh plan, diameter of cell 42 μ. *b*. Areolation.

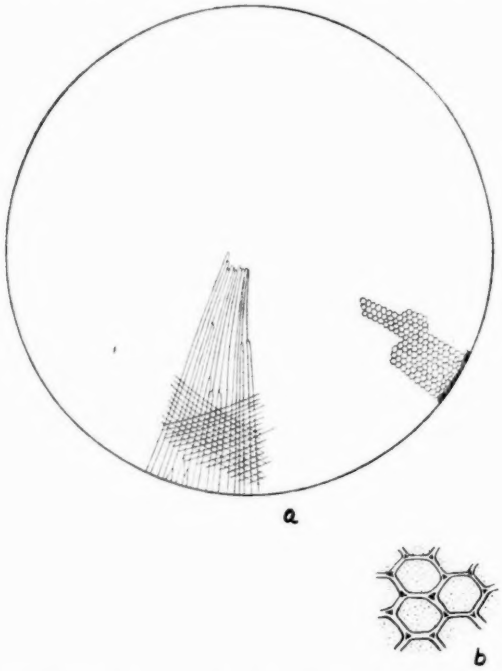

FIG. 15.—*Coscinodiscus gigas*. *a*. Mesh plan, diameter of cell 340 μ. *b*. Areolation.

of areolae usually distinct. Meshes straight in tangential lines based upon six sectors. Marginal spinulae present.

Group 4. Radiati.

Species 4. **Coscinodiscus gigas** Ehrenberg (37, 1841, p. 412).

Synonyms:

Coscinodiscus radiatus Bailey (7, 1842, XLII), *Coscinodiscus giganteus* Péragallo (97, 1878, p. 433).

Cells coin-shaped, weakly siliceous, diameter 300–500 μ. Valves flat, covered with radial areolation. Fairly large, irregular, hyaline area in centre. Areolae increase in size from centre to periphery. Numerous, small, rounded chromatophores.

Species 5. **Coscinodiscus radiatus** Ehrenberg (37, 1839, p. 148).

Synonyms:

C. borealis Ehrenberg (37, 1861, p. 294), *C. fallax* Schumann (106, 1876, p. 62), *C. caspius* Ehrenberg (37, 1873, p. 394), *C. radiatus* f. *minor* A. Schmidt (103, 1875, pl. 3, f. 34), *C. radiatus* f. *parva* Grunow (56, 1878, p. 124), *C. radiatus* var. *subaequalis* Grunow (56, 1884, p. 20), *C. radiatus* var. *borealis* Grunow (56, 1884, p. 20), *C. radiatus* var. *media* Grunow (56, 1884, p. 20), *C. radiatus* var. *glacialis* Grunow (56, 1884, p. 20).

Cells coin-shaped, valves flat. Diameter 35–60 μ. Valves coarsely areolated, lacking rosette or central area. Areolae 3–4 in 10 μ in centre, 6–7 in 10 μ at margin. Radial rows distinct, secondary rows spiral, usually indistinct. Valve margin small.

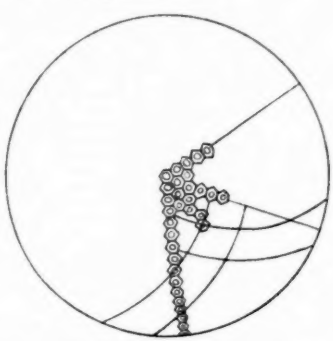

Fig. 16.—*Coscinodiscus radiatus.* Diameter of cell 42 μ.

Species 6. **Coscinodiscus janischii** A. Schmidt
(103, 1875, pl. 64, fs. 3, 4).

Synonym: *Coscinodiscus marginatus* Janisch (66, 1862, p. 3) (nec Ehrenberg).

Cells large, discoid. Irregularly hexagonal areolae, equal in size, arranged in radial rows. Regularity of hexagons deteriorates toward valve centre. Clear central area about $\frac{1}{10}$ total radius. Fascicules or

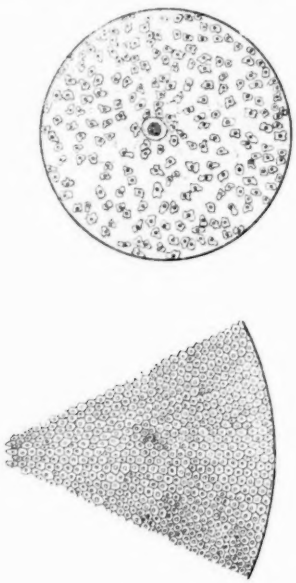

FIG. 17.—*Coscinodiscus janischii*. After Karsten, 1905.

wedges lacking but rows of single cells are regularly placed. Oblique rows less clear. Diameter 160–360 μ. Chromatophores irregular plates arranged on entire valve surface, each with one rectangular pyrenoid.

Apparently a surface form, it occurs most abundantly in 10–20 m. near Capetown and elsewhere. Reported from this area by Karsten.

Species 7. **Coscinodiscus rotundus** Karsten
(68, 1905, p. 154).

Valves strongly convex, centres slightly concave. Radial rows run straight to the margin; similar to *Coscinodiscus convergens* but smaller.

Hexagonal areolations 10 in 10 μ at centre, 6 in 10 μ at half-radius. At margin very small, almost "pearl-shaped" hexagons. Diameter 78 μ. Chromatophores numerous cocciform bodies, mostly lying against the valves.

Described from this area by Karsten.

FIG. 18.—*Coscinodiscus rotundus.* Valve view. Partly after Karsten, 1905.

Species 8. **Coscinodiscus varians** Karsten (68, 1905, p. 155).

Small form with convex valves. In valve view the central rosette is formed by a single, larger hexagon. Areolae in radiating rows, starting

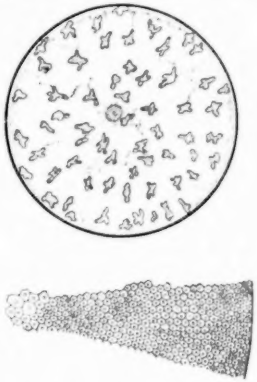

FIG. 19.—*Coscinodiscus varians.* After Karsten, 1905.

small but increasing considerably in size outward until at about half-valve radius the rows divide, after which the areolae are again smaller but increase in size toward the valve margin, where further division of the rows occurs with consequent diminution in size of areolae. Diameter 70–90 μ. Chromatophores oblong to biscuit-shaped, closely arranged on valve surface.

Described from this region by Karsten.

Species 9. **Coscinodiscus granii** Gough

(46, 1905, p. 338).

Synonyms:

Coscinodiscus concinnus Miquel (87, 1894, pl. 8, fs. 10, 13), *Coscinodiscus* sp. nov. Gough (46, 1903, p. 224).

Cells discoid in valve view, cuneiform in girdle view. Mesh consists of fine lines radiating from definite central rosette, secondary spiral rows distinct. Areolae diminish in size towards valve margin. Marginal spinulae, 5–7 μ apart, with distinct hyaline lines radiating from them toward the centre. Two asymmetrically placed apiculi on valve margin. Valves arched, centres excentric, girdle cuneate. Chromatophores numerous rounded bodies. Diameter 100 μ.

Neritic. Reported at two stations off South-West Africa by Hendy.

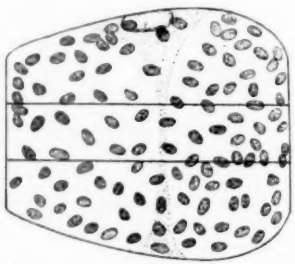

Fig. 20.—*Coscinodiscus granii*. Girdle view. After Gran and Angst, 1931.

Group 5. Fasciculati.

Species 10. **Coscinodiscus curvatulus** Grunow

(103, 1875, pl. 57, f. 33).

Synonyms:

Odontodiscus curvatulus Grunow (24, 1883*a*, p. 488), *Coscinodiscus curvatulus* var. *inermis* Grunow (56, 1884, p. 83), *Coscinodiscus curvatulus* var. *genuina* Grunow (56, 1884, p. 83).

Cells discoid, solitary. Valves almost flat, areolated. Meshes arranged in curved sectors. First curved line of each sector radiates from centre.

Other meshes of sector parallel with it. Central area surrounded by ring-like groove. No spinulae or apiculi. Diameter of valve 40–100 μ.

FIG. 21.—*Coscinodiscus curvatulus*. Diameter of cell 57 μ.

Species 11. **Coscinodiscus subtilis** Ehrenberg
(37, 1843*a*, p. 412).

Synonym: *Coscinodiscus normani* Gregory (52, 1859, p. 80).

Cells discoid. Valves thin, flat, with fine areolation. Central area and rosette lacking. Mesh consists of indistinct, radiating fascicules of

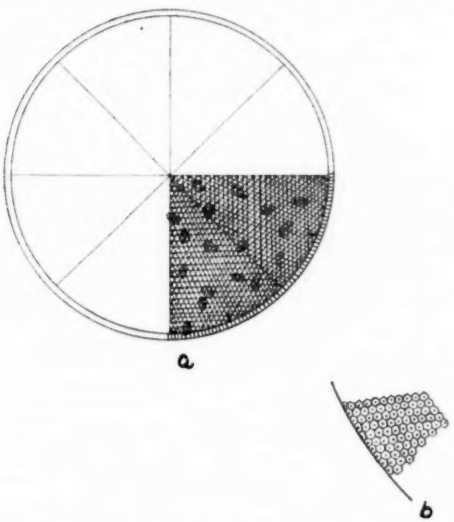

FIG. 22.—*Coscinodiscus subtilis*. *a*. Valve view showing mesh plan. *b*. Areolation at border. Altered from Karsten, 1905.

parallel lines crossed by more distinct oblique rays. Marginal spinulae present but indistinct. Girdle simple, striate, narrow. Chromatophores numerous plate-like bodies. Diameter 80–130 μ.

Neritic. Reported as occurring occasionally around the Cape of Good Hope by Hendy.

Genus II. **PLANKTONIELLA** Schütt
(93, 1893, p. 20).

Only species in this genus.

Species 1. **Planktoniella sol** (Wallich) Schütt
(93, 1893, p. 20).

Synonyms:

Coscinodiscus sol Wallich (103, 1860, p. 38), *Cestodiscus sol* Grunow (102, 1880, pl. 129, f. 6), *Planktoniella woltereckii* (Schimp.) Karsten (57, 1905, p. 157).

Cells coin-shaped, single, with a hyaline wing all around of extracellular chambers strengthened by radial rays. This expansion is weakly siliceous. Valves are flat and areolated like *Coscinodiscus excentricus*. Areolae are smaller near the margin. Numerous, small, plate-like chromatophores. Diameter of entire cell 50–165 μ.

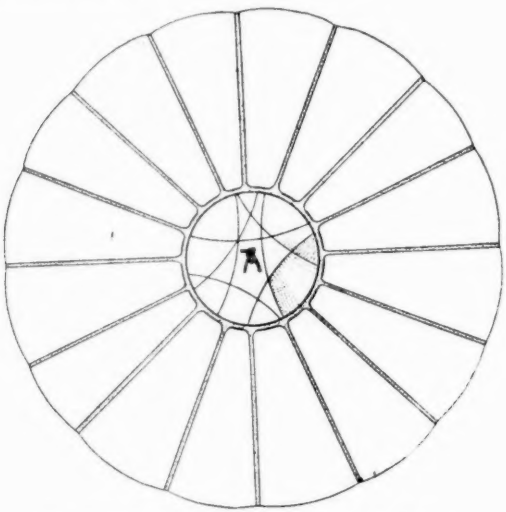

FIG. 23.—*Planktoniella sol*. Diameter of cell 83 μ.

Genus III. **ACTINOCYCLUS** Ehrenberg
(37, 1839, p. 171).

Cells solitary, *Coscinodiscus*-like. Valves with radial rows of points, marginal spinulae and one transparent "eye" near the margin inside the spinulae.

Species: *A. octonarius.*
A. rotula.

Species 1. **Actinocyclus octonarius** Ehrenberg
(37, 1839, p. 172).

Synonym: *Actinocyclus ehrenbergii* Ralfs in Pritchard (100, 1861, p. 834).

Cells discoid, valves convex, strongly rounded at margins, flattened in centre, thick-walled. Valve furnished with a crown of marginal spinulae from which run rows of puncta toward the centre, dividing the valve into radial compartments each containing a fascicule of radial lines of puncta. The dividing rows are surrounded by hyaline, interfascicular spaces. Marginal zone finely, radially striated. Girdle smooth, no intercalary bands. Diameter 170–220 μ. Chromatophores numerous, small plates.

Neritic, cosmopolitan. Reported here by Hendy.

FIG. 24.—*Actinocyclus octonarius.* Portion of valve. Altered from Péragallo in Lebour, 1930.

This is the type-species of the genus. It was originally split into a number of species by Ehrenberg, which were later lumped by Ralfs (100, 1861, p. 834) under the title "*Actinocyclus ehrenbergii*" new species. The illegality of this was pointed out by Hendy (62, 1937, p. 263), who reinstated the present combination.

Species 2. **Actinocyclus rotula** Brun

(19, 1891, p. 6).

Cells discoid. Valves flat, divided into 12–16 segments by radial lines of granules, which terminate in apiculi at valve margin. Small central

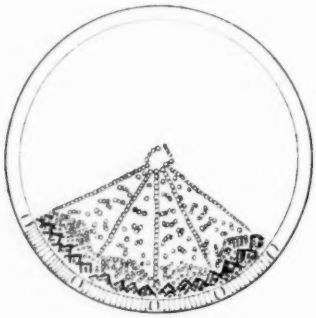

FIG. 25.—*Actinocyclus rotula.* Drawn from portion of photomicrograph in J. Brun, 1891.

hyaline area present. Interstitial segments irregularly and sparsely punctate. Marginal zone strong, radially striate. Diameter 66 μ. Chromatophores numerous, small plates.

Reported here by Hendy.

2. ACTINODISCEAE Schütt.
   a. Actinoptychinae Schütt.
   Genus: I. *Actinoptychus.*

Genus I. **ACTINOPTYCHUS** Ehrenberg

(37, 1841, p. 400).

Cells disc-shaped, solitary. Valve divided into alternately raised and depressed sectors. Smooth central field. No intercalary bands. One or more claw-like processes on outer margin of sectors, often only on raised ones.

Species: *A. senarius.*
A. splendens.
A. vulgaris.

Species 1. **Actinoptychus senarius** (Ehrenberg) Ehrenberg
(37, 1843*a*, pl. 1, f. 27).

Synonyms:

Actinocyclus senarius Ehrenberg (37, 1838, p. 172), *Actinocyclus undulatus* Kützing (70, 1844, p. 132), *Actinoptychus undulatus* (Bailey) Ralfs (100, 1861, p. 839), *Actinoptychus undulatus* Bailey (7, 1842, pl. 2, f. 11), *Actinoptychus biternarius* Ehrenberg (37, 1843*b*, p. 166), *Omphalopelta areolata* Ehrenberg (37, 1844, p. 270), *Actinoptychus omphalopelta* Grunow (56, 1868, p. 25), *Actinoptychus areolatus* A. Schmidt (103, 1875, pl. 1, f. 9), *Actinoptychus delectus* A. Schmidt (103, 1875, pl. 1, f. 8).

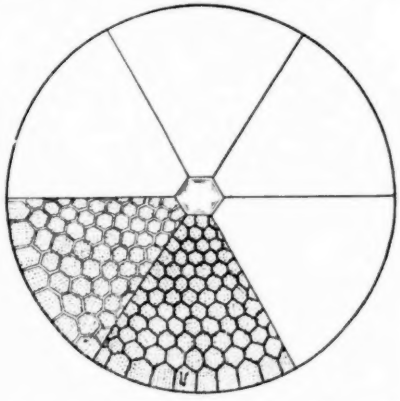

FIG. 26.—*Actinoptychus senarius*. Diameter of cell 72 μ.

Cells discoid, diameter 40–130 μ. Valves with six radial sectors, alternately raised and depressed. Irregular, coarse, polygonal areolation. Inner surface of areoles punctated. Smooth, hexagonal central field. Each raised sector, occasionally all the sectors, furnished with a stout apicule near the valve margin.

This is the type-species of the genus and is called *Actinoptychus undulatus* (Bailey) Ralfs by Hustedt (1930) and Cupp (1943), and *Actinoptychus undulatus* (Bailey) by Lebour (1930). However, Hendy (1937) points out that Ehrenberg's epithet claims priority.

Species 2. **Actinoptychus splendens** (Shadbolt) Ralfs ex Pritchard
(100, 1861, p. 840).

Synonyms:

Actinosphaenia splendens Shadbolt (108, 1854, p. 16), *Actinoptychus sedenarius* Ehrenberg (37, 1854, pl. 18, f. 26), *Actinoptychus quatuodrenarius*

Ehrenberg (37, 1854, pl. 18, f. 25), *Halionyx quinarius, senarius, octonarius, nonarius, denarius, undenarius, vicenarius* Ehrenberg (37, 1862, pp. 9–10), *Actinoptychus glabratus* Grunow (119, 1880, pl. 120, f. 6).

Cells discoid. Valves radially undulate, divided into 10–20 sectors.

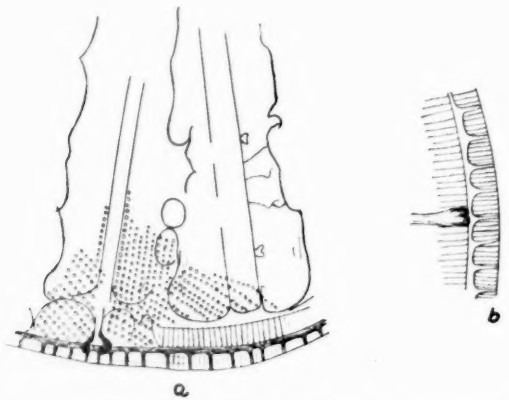

FIG. 27.—*Actinoptychus splendens*. *a*. Section of valve near margin. *b*. Section of margin. After Cupp, 1943.

Nearly circular central area present. Valves coarsely, polygonally areolated. On each raised sector is a stout marginal apicule from which runs a hyaline line toward the central area. Each depressed sector has a narrow marginal hyaline band and lacks apiculi. Valve margin strongly striate. Diameter 120–140 μ. Chromatophores numerous, plate-like bodies.

Oceanic. Reported by Hendy as occurring rarely off the South African coast.

Species 3. **Actinoptychus vulgaris** Schumann
(106, 1867, p. 64).

Cells discoid. Valves divided into 6–20 sectors. Clear central area present. Mesh consists of a primary pattern of decussate rows of fine puncta over which is a more or less clear, coarse areolation. Margin clear and outer margin crenated. Diameter 64–116 μ. Chromatophores numerous, plate-like bodies.

Reported from this region by Karsten.

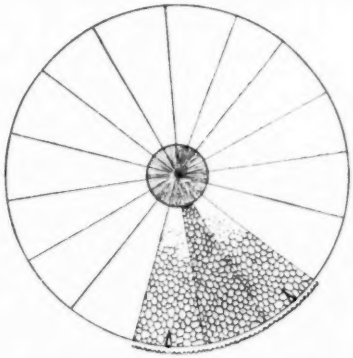

FIG. 28.—*Actinoptychus vulgaris.* Partly after Karsten, 1905.

b. Asterolamprinae Schütt.
Genus: I. *Asteromphalus.*

Genus I. **ASTEROMPHALUS** Ehrenberg
(37, 1844, p. 198).

Cells discoid or slightly oval, solitary. Valves flat to slightly convex, areolated. Central hyaline area with raised hyaline rays radiating from it. One ray narrower than the others.

Species: *A. heptactis.*
A. hookerii.

Species 1. **Asteromphalus heptactis** (Brébisson) Ralfs
(100, 1861, p. 838).

Synonyms:

Spatangidium heptactis Brébisson (16, 1857, p. 296), *Asterolampra heptactis* Greville (53, 1860*b*, p. 122), *Asteromphalus reticulatus* Cleve (24, 1873, p. 5), *Asteromphalus ornithopus* Karsten (68, 1905, p. 90), *Asteromphalus ralfsianus* Grunow (103, 1875, pl. 38, f. 5).

Cells solitary, slightly oval. Valves slightly convex. Seven rays of unequal length, with one long, narrow ray and three broader rays on either side. Hyaline area slightly excentric, diameter one-quarter to one-third that of diameter of valve. Diameter of valve 50–110 μ.

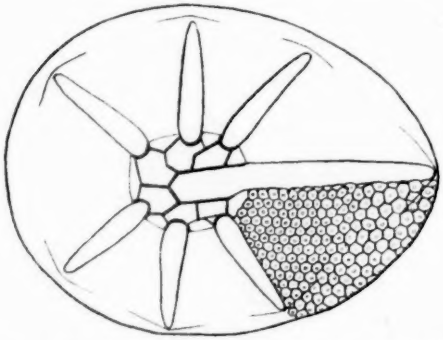

FIG. 29.—*Asteromphalus heptactis.* Diameter of cell 81 μ.

Species 2. **Asteromphalus hookeril** Ehrenberg (37, 1844, p. 200).

Synonyms:

Asteromphalus buchii Ehrenberg (37, 1844, p. 200), *Asteromphalus cuvierii* Ehrenberg (37, 1844, p. 200), *Asteromphalus humboldtii* Ehrenberg (37, 1844, p. 200), *Asterolampra hookerii* Greville (53, 1860*b*, p. 114),

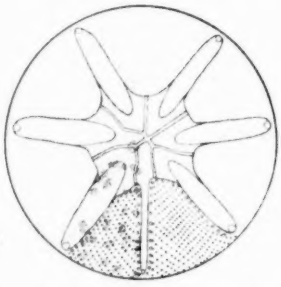

FIG. 30.—*Asteromphalus hookerii.* Partly after Karsten, 1905.

Asteromphalus regularis Karsten (68, 1905, p. 90), *Asteromphalus brookei* Bailey in (68, 1905, p. 90).

Cells discoid. Valves somewhat convex, undulate, divided into sectors by five to seven, narrow, hyaline rays. Hyaline central area about half total diameter. Sectors finely areolated. Central area marked by radiating branched lines. Diameter 44–60 μ.

Oceanic. Reported from this area by Karsten.

II. **Solenoideae** Schütt.
3. Solenieae Schütt.
a. Lauderiinae Schütt.
Genera: I. *Corethron*.
II. *Schröderella*.
III. *Leptocylindrus*.

Genus I. **CORETHRON** Castracane
(23, 1866, p. 85).

Cells solitary, cylindrical with rounded valves bearing a marginal crown of slender spines directed outwards at an angle. Numerous indistinct intercalary bands.

Species: *C. criophilum*.

Species 1. **CORETHRON criophilum** Castracane
(23, 1886, p. 85).

Synonyms:

Corethron hystrix Hensen (63, 1887, p. 89), *Corethron valdiviae* Karsten (68, 1905, p. 101), *Corethron inerme* Karsten (68, 1905, p. 104), *Corethron*

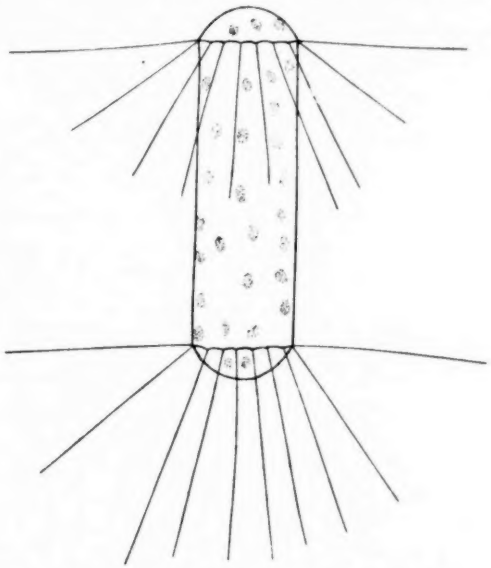

Fig. 31.—*Corethron criophilum*. Diameter of cell 22 μ.

murrayanum Castracane (23, 1886, p. 86), *Corethron pelagicum* Brun (19, 1891, p. 20), *Corethron hispidum* Castracane (23, 1886, p. 86).

Cell walls fairly thick. Valves strongly convex and furnished with a marginal circlet of well-developed spines. Intercalary bands very difficult to see. Numerous rounded, plate-like chromatophores.

Hendy 1937 lists the above synonyms for *C. criophilum*. He considers *Corethron* to be a monotypic genus with *C. criophilum* as the type-species. The other forms are not given the dignity of species but are considered as phases of the type-species, and are designated by the well-known epithets of the species which they replace. The close relationship of these forms, and indeed the synonymity of some, has been noted before by Ostenfeld 1902, Mangin 1915, Hustedt 1930, Gran and Angst 1931, and Hart 1934. Cupp 1943 did not use Hendy's terminology. The synonymy is quoted here although the term "phase" is not used in this report. The form occurred infrequently in these collections.

Genus II. **SCHRÖDERELLA** Pavillard
(95, 1913, p. 126).

Cells cylindrical. Valves flat to slightly convex, with concavity in the centre. A spine in this concavity unites with a corresponding spine of the adjacent cell. Valve margin armed with a crown of spinulae each with two gelatinous threads joining corresponding threads of adjacent cell. Numerous minutely punctated intercalary bands.

Species: *S. delicatula.*

Species 1. **Schröderella delicatula** (Péragallo) Pavillard
(95, 1913, p. 123).

Synonyms:

Lauderia delicatula Péragallo (96, 1888, p. 81), *Detonula delicatula* Gran (47, 1900*b*, p. 112), *Lauderia schröderi* Bergon (9, 1903*a*, p. 69), *Detonula schröderi* Gran (47, 1905, p. 22), *Schröderella schröderi* (Bergon) Pavillard (95, 1925, p. 23).

Cells cylindrical, united in dense rigid chains. Valves flat to slightly convex with depression in centre. Diameter of cell 18–30 μ. Mantle surface delicately areolated. Numerous collar-like intercalary bands.

Genus III. **LEPTOCYLINDRUS** Cleve
(24, 1889, p. 54).

Cells long, cylindrical, united by whole valve surface to form chains. Valves flat, unarmed. Intercalary bands difficult to see. Cell walls thin, hyaline. One to many chromatophores.

Species: *L. danicus.*

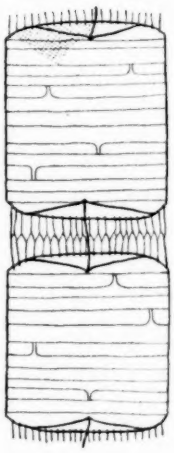

FIG. 32.—*Schröderella delicatula.*
Diameter of cell 21·6 μ.

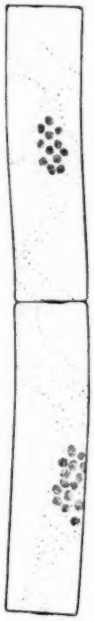

FIG. 33.—*Leptocylindrus danicus.*
Diameter of cell 10·6 μ.

Species 1. **Leptocylindrus danicus** Cleve

(24, 1889, p. 54).

Cells cylindrical, 6–12 μ in diameter, 2–10 times as long. Long stiff chains, often only one cell wall between two valves. Chromatophores numerous. Intercalary bands very difficult to see.

b. Rhizosoleniinae Schütt.
Genera: I. *Guinardia.*
II. *Rhizosolenia.*

Genus I. **GUINARDIA** H. Péragallo

(96, 1892, p. 107).

Cells cylindrical, longer than broad. Solitary or in chains. Intercalary bands numerous, collar-like. Valves circular, flat. A small, rudimentary

spine is placed asymmetrically at the valve margin. Numerous chromatophores. Nucleus in central cytoplasm.

Species: *G. flaccida.*
G. blavyana.

Species 1. **Guinardia flaccida** (Castracane) H. Péragallo (96, 1892, p. 107).

Synonyms:

Eucampia striata var. *maxima* Stolterfoth (114, 1879, p. 825), *Rhizosolenia ? flaccida* Castracane (23, 1886, p. 74), *Pyxilla baltica* Hensen (63, 1887, p. 87), *Rhizosolenia castracane* Cleve (24, 1889, p. 2), *Henseniella baltica* Schütt (33, 1894, p. 1425), *Guinardia baltica* Schütt (107, 1896, p. 84).

Cells cylindrical, solitary or in chains. Valves slightly concave with asymmetrical, rudimentary tooth at margin. Diameter of cell 30–90 μ. Numerous narrow intercalary bands. Cell wall very weakly siliceous. Numerous chromatophores, usually stellate but frequently rounded.

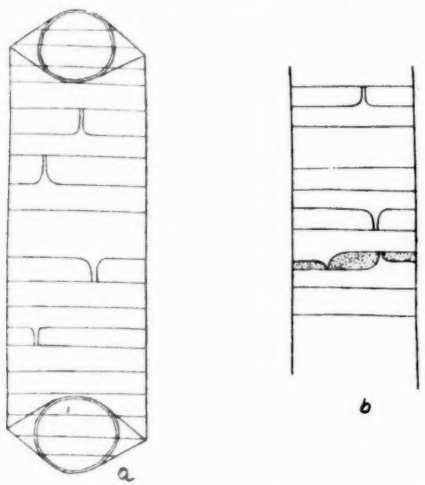

Fig. 34.—*Guinardia flaccida*. *a*. Single cell, diameter 70·2 μ.
b. Junction of cells in chain.

Species 2. **Guinardia blavyana** H. Péragallo (96, 1892, p. 107).

Synonym: *Guinardia blavyana* var. *conspicua* Péragallo (96, 1892, p. 107).

Cells solitary or united in chains of two or three. Collar-like intercalary bands with overlapping angular ends. Chromatophores discoid,

each with a pyrenoid. Nucleus central, with radiating cytoplasmic threads.

Reported from here by Karsten, who considers the nature of the intercalary bands places the species near "Dactyliosolen".

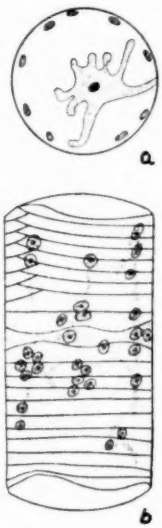

FIG. 35.—*Guinardia blavyana*. *a*. Cell with nucleus. *b*. Cell showing contents. After Karsten, 1905.

Genus II. **RHIZOSOLENIA** (Ehrenberg) Brightwell (18, 1858*a*, p. 93).

Cells cylindrical, elongated pervalvar axis. Usually straight, sometimes curved. Solitary or in chains. Valves circular or elliptical, with an excentric apex or process which fits into a corresponding trough on the adjacent cell. Intercalary bands very numerous but sometimes difficult to see. Chromatophores usually numerous. Several species have a tendency to dimorphism, e.g. *R. alata*. These forms are considered by different authors as different species or as forms of the same species. Hendy (1937) reduces them to synonyms and regards them as "phases" of the same species.

The genus is subdivided according to the form of the valve and the intercalary bands. Pavillard's (1925) scheme is followed here.

KEY TO SPECIES.

Group 1. **Inermes.** Valves more or less conical, truncated, without terminal spine. Scales as in Genuinae . . . . . *R. alata.*

Group 2. **Affines.** Valves rounded, not conical, furnished with a short spine. Intercalary bands collar-like.

A. Cells straight.

B. Chromatophores small, numerous; valves irregularly arched . . . . . *R. fragilissima.*

C. Chromatophores few, large; valves flat . . . *R. delicatula.*

A_1. Cells curved . . . . . *R. stolterfothii.*

Group 3. **Robustae.** Valves elongated and conical. Extremity more or less thickened with a variably shaped spine. Intercalary bands collar-like . . . . . *R. robusta.*

Group 4. **Imbricatae.** Two rows of lateral scale-like intercalary bands. Suture lines zigzag when spine is dorsal . . . . . *R. imbricata.*

Group 5. **Genuinae.** Two rows of dorsi-ventral scale-like intercalary bands.

A. Two wing-like expansions at base of spine . . *R. styliformis.*

B. Wing-like expansions lacking . . . . . *R. hebetata.*

Group 6. **Squamosae.** Intercalary bands numerous, imbricated scales . *R. simplex.*

GROUP 1. INERMES.

Species 1. **Rhizosolenia alata** Brightwell

(18, 1858*a*, p. 96).

Cells cylindrical, straight. Valves conical, narrowing suddenly to a tube-like, more or less curved, oblique process. At the base of the tube

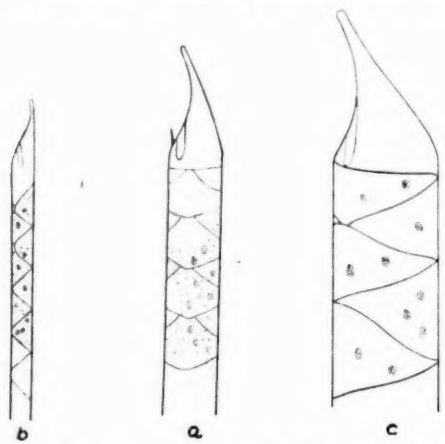

FIG. 36.—*a. Rhizosolenia alata.* Diameter of cell 9 μ. *b.* form "gracillima." Diameter of cell 5 μ. *c.* form "indica." Diameter of cell 32 μ.

is a depression into which the apex of the adjacent cell fits. Intercalary bands scale-like, rhombic, in two dorsi-ventral rows, finely striated. Cell wall thin, weakly siliceous. Chromatophores numerous, small. Diameter of cell 7–15 μ.

Form "**gracillima**" (Cleve) Grunow (119, 1880, pl. 79, f. 8).

Synonym: *Rhizosolenia* (*alata* var.?) *gracillima* Cleve (24, 1881, p. 26).

Structurally similar to type but very much narrower. Diameter of cell 4–7 μ.

Form "**indica**" (Péragallo) Ostenfeld (93, 1901*b*, p. 160).

Synonyms:

Rhizosolenia indica Péragallo (96, 1892, p. 116), *Rhizosolenia quadriiuncta* Péragallo (96, 1892, pl. 5, f. 17), *Rhizosolenia alata* var. *corpulenta* Cleve (24, 1897*a*, p. 24).

Structurally similar to type but having a very much greater diameter. Diameter of cell 20–60 μ.

Group 2. Affines.

Species 2. **Rhizosolenia delicatula** Cleve (24, 1900, p. 28).

Cells cylindrical, with flat valves slightly rounded on margins. Closely set, straight chains. Valve armed with a short excentric spine fitting into the margin of the neighbouring cell. Chromatophores few, large. Diameter of cell 10–12 μ.

Species 3. **Rhizosolenia stolterfothii** H. Péragallo (96, 1888, p. 82).

Synonyms:

Eucampia striata Stolterfoth (114, 1878, p. 835), *Pyxilla stephanos* Hensen (63, 1887, p. 88).

Cells cylindrical, united in curved chains. Valves flat, armed with a strong spine visible only at the free ends. Intercalary bands collar-like, numerous, usually easily seen. Chromatophores small, numerous. Diameter of cell 15–45 μ.

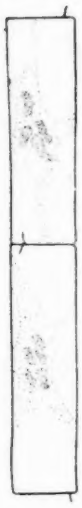

FIG. 37.—*Rhizosolenia delicatula.*
Diameter of cell 16 μ.

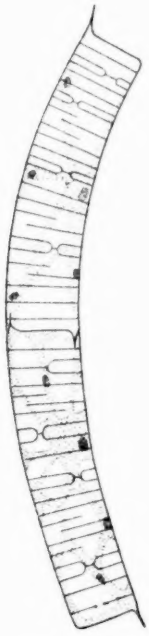

FIG. 38.—*Rhizosolenia stolterfothii.*
Diameter of cell 27 μ.

Species 4. **Rhizosolenia fragilissima** Bergon
(9, 1903*a*, p. 49).

Synonyms:

Rhizosolenia cylindrus Ostenfeld (93, 1899, p. 55), *Leptocylindrus danicus* Schütt (107, 1900, p. 504), *Rhizosolenia delicatula* Gran (47, 1902, p. 172), *Rhizosolenia delicatula* Ostenfeld (93, 1903, p. 568, f. 123), *Rhizosolenia faeroëensis* Ostenfeld (93, 1903, p. 568, f. 124), *Rhizosolenia pellucida* Schröder (104, 1911, p. 631, f. 6).

Cells cylindrical, 8–70 μ in diameter, ends rounded, united in short straight chains. In the centre of the valve is a short spine fitting into a corresponding depression on the adjacent cell. Collar-like intercalary bands, cell wall weakly siliceous. Chromatophores numerous, small plates.

FIG. 39.—*Rhizosolenia fragilissima.* Diameter of cell 13·5 μ.

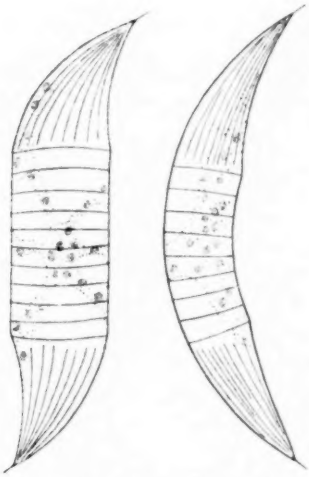

FIG. 40.—*Rhizosolenia robusta.* Diameter of cell 55 μ.

GROUP 3. ROBUSTAE.

Species 5. **Rhizosolenia robusta** Norman (99, 1861, p. 866).

Synonym: *Rhizosolenia sigma* Schütt (107, 1893, p. 22).

Cells cylindrical, with deeply conical, curved valves. Valvar plane elliptical. Small, hollow, apical process with short spine. Cells usually single, crescent- or **S**-shaped. Diameter of cell 50–400 μ. Intercalary bands numerous, collar-like. Chromatophores numerous.

GROUP 4. IMBRICATAE.

Species 6. **Rhizosolenia imbricata** var. **shrubsolei** (Cleve) Schröder (104, 1906*a*, p. 346).

Synonyms:

Rhizosolenia shrubsolei Cleve (24, 1881, p. 26), *Rhizosolenia atlantica* Péragallo (96, 1892, p. 114), *Rhizosolenia pacifica* Péragallo (96, 1892, fs. 6, 7).

Cells cylindrical, single or in chains. Valves oblique, pointed, with

apical process hollow nearly all the way up, with small wings at the base which run up about a third of the spine and do not extend to the valve. Intercalary bands scale-like in two long rows, each band being a triangular scale with the corner pointing upwards so that they form an imbricating row on each side of the apex. The bands have striations formed of minute puncta. Chromatophores numerous, small. Diameter of cell 12–22 μ.

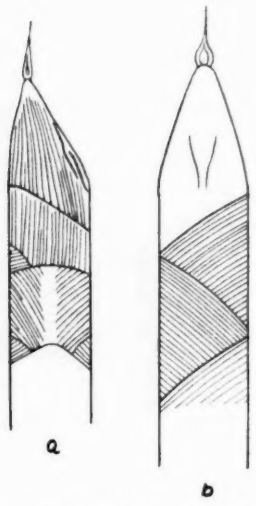

FIG. 41.—*Rhizosolenia imbricata* var. *shrubsolei*. *a*. Side view of cell, diameter 18 μ. *b*. Ventral view of cell.

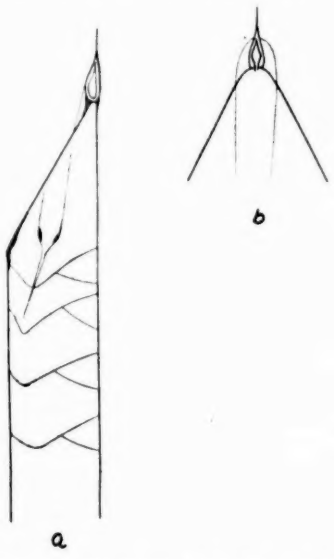

FIG. 42.—*Rhizosolenia styliformis*. *a*. Side view of cell, diameter 77 μ. *b*. Ventral view of end of cell.

GROUP 5. GENUINAE.

Species 7. **Rhizosolenia styliformis** Brightwell

(18, 1858*a*, p. 95).

Cells cylindrical. Valves obliquely pointed as in *R. imbricata* var. *shrubsolei*, but more sharply. Valve process pointed, hollow, with cavity penetrating valve. Two wing-like processes begin on the valve and finish near the base of the process. Valve has a groove for the spine and wings of the adjacent cell. Intercalary bands scale-like with reticulated sculpturing. Very numerous chromatophores. Diameter of cell 40–100 μ.

Species 8. **Rhizosolenia hebetata** (Bailey) Gran emend (47, 1904, p. 524).

This is a dimorphic species. Occasionally a cell exhibits a different form at each end.

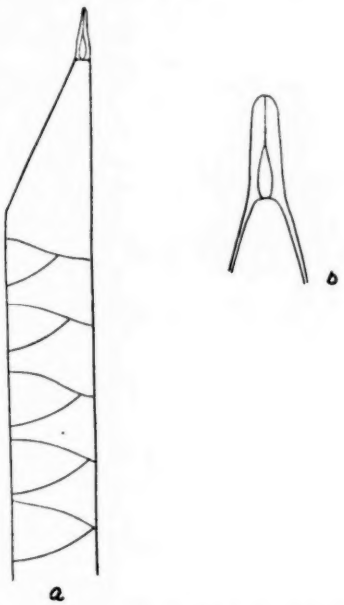

FIG. 43.—*Rhizosolenia hebetata* form *hiemalis*. *a*. Part of cell, diameter 18 μ. *b*. Spine.

Form "**hiemalis**" Gran (47, 1904, p. 527).

Synonyms:

Rhizosolenia hebetata Bailey (8, 1856, p. 5), *Rhizosolenia hebetata* var. *subacuta* Grunow (56, 1884, p. 527).

Cells straight, valves drawn out longitudinally. Thick, solid, apical process with small, hollow, rounded spine. Intercalary bands distinct. Cell wall strongly siliceous. Chromatophores small, numerous. Diameter of cell 18–20 μ.

Form "**semispina**" (Hensen) Gran (47, 1905, p. 55).

Synonym: *Rhizosolenia semispina* Hensen (63, 1887, p. 84).

Cells cylindrical, valves drawn out, armed with long, curved, hair-like spine. Similar to form "hiemalis" but smaller in diameter, 5–12 μ, and more weakly siliceous. Imbrications more delicate in structure.

Occurs infrequently in the northern part of this area.

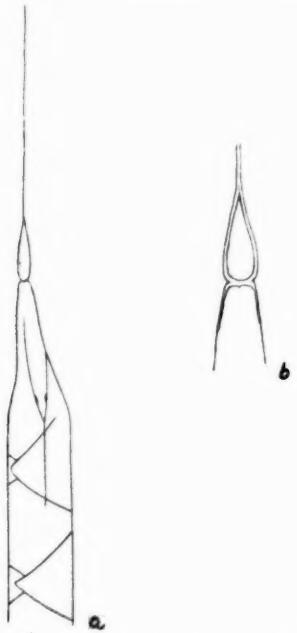

Fig. 44.—*Rhizosolenia hebetata* form *semispina*. *a*. Cell in ventral view. *b*. Base of spine.

Group 6. Squamosae.

Species 9. **Rhizosolenia simplex** Karsten (68, 1905, p. 95).

Cells small, cylindrical, straight. Valve deeply conical, with slender spine hollow at the base. Intercalary bands small, squamose, scale-like. Cell wall very weakly siliceous, imbrications very difficult to see. Chromato-

phores numerous cocciform bodies, arranged along cell wall and around nucleus. Diameter 10–26 μ. Length 200–400 μ.

Oceanic. Reported by both Karsten and Hendy as being fairly common in this area.

III. **Biddulphioideae** Schütt.

4. Chaetocerae Schütt.

Genera I. *Bacteriastrum.*

II. *Chaetoceros.*

Genus I. **BACTERIASTRUM** Shadbolt

(108, 1854, p. 14).

Cells cylindrical. Valves armed with marginal bristles. The fusion of the bristles of one cell with those of the next forms loose chains. The bristles of neighbouring cells are fused for a certain length outside the base and then bifurcate. Terminal bristles often curved in valve view, not fused and therefore not forked. Pavillard revised the genus 1924–25.

Group 1. Isomorpha.

Terminal setae of like construction and form on both ends of the chain. Terminal setae directed either outward or toward the centre of the chain.

Group 2. Sagittata.

Terminal setae on either end of the chain different in form and direction. Setae of posterior valve directed outward from chain and running nearly parallel with chain axis. Setae of anterior valve curved toward inner part of chain, or deviating little from valvar plane.

Species: *B. hyalinum.*

Group I. Isomorpha.

Species 1. **Bacteriastrum hyalinum** Lauder

(71, 1864, p. 6).

Synonyms:

Bacteriastrum spirillum Castracane (23, 1886, pl. 29, f. 1), *Bacteriastrum varians* var. *borealis* Ostenfeld (93, 1901*a*, p. 293), *Bacteriastrum minus* Karsten (68, 1905, p. 171).

Cells not much longer than broad. Chain straight or slightly curved. Apertures narrow but distinct. Number of inner setae per valve 7–25. Bifurcations parallel with chain axis. Terminal setae curved and bent toward chain centre. Chromatophores numerous, small. Diameter of cell 13–56 μ.

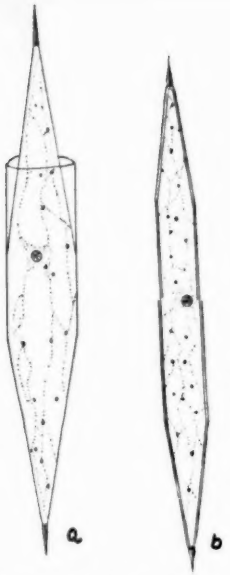

FIG. 45.—*Rhizosolenia simplex.* After Karsten, 1905.

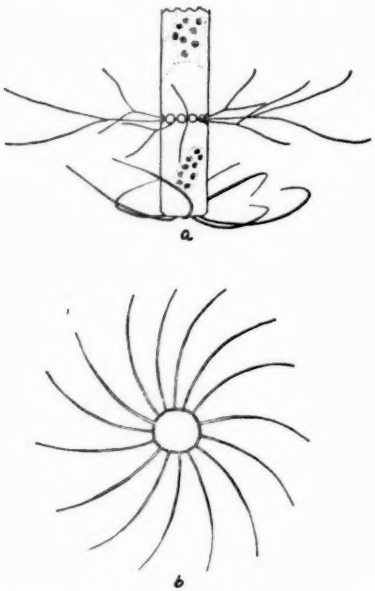

FIG. 46.—*Bacteriastrum hyalinum.* *a.* End of chain. Diameter of cell 23 μ.
b. Valve view of terminal cell.

Genus II. **CHAETOCEROS** Ehrenberg (37, 1844).

Cells oval to nearly circular in valve view. Quadrangular in broad girdle view. Occasionally solitary, usually united by setae into long or short chains. Valve surface flat with setae on the pointed ends of the ellipse. These setae cross the setae of the adjacent cell and fuse firmly. Cells separated by large or small apertures or foramina. Special end cells bear the terminal setae which are usually shorter and thicker. Cell wall formed of two valves and one or two girdle bands. Intercalary bands sometimes present but usually difficult to see. One to several, small or large, chromatophores. Pyrenoids sometimes visible. Resting spores formed in most neritic species. The valves of the spores are often armed with spines or spicules.

The genus is subdivided as follows:

Sub-genus 1. PHAEOCEROS Gran (47, 1897*a*).

Large, robust species. Chromatophores numerous, globoid, and penetrating into setae.

Sec. 1. **Atlantica** Ostenfeld (93, 1903).

Direction of all setae alike in one plane, except terminal setae which differ from others. Small spine usually present in centre of valve.

1. *C. atlanticum.*

Sec. 2. **Borealia** Ostenfeld (93, 1903).

Setae usually diverging in all directions, the directions on one valve often differing from those on the other. Usually no spine in centre of valve.

2. *C. peruvianus.*
3. *C. convolutum.*

Sub-genus 2. HYALOCHAETE Gran (47, 1897*a*).

Chromatophores one or several plates, more seldom numerous granules. Setae usually thin without chromatophores in them. Chiefly neritic. Resting spores known in most of the species.

A. *Each cell with more than two chromatophores.*

Sec. 1. **Oceanica** Ostenfeld emen. Lebour (73, 1930).

Chromatophores rather large, 6–10. Setae fused along a short portion of their length. No resting spores known. Oceanic.

4. *C. decipiens.*

Sec. 2. **Dicladia** (Ehrenberg) Gran emen. Lebour (73, 1930).

Like *Oceanica*, but with setae not always fused for a portion of their length. Resting spores with two horns armed with small branches on primary valves. Neritic.

5. *C. capense.*
6. *C. lorenzianus.*
7. *C. tetras.*

Sec. 3. **Cylindrica** Ostenfeld (93, 1903).

Valves nearly circular. Apertures very narrow. Chromatophores small, numerous. Terminal setae not thicker than others. Resting spores about the middle of the cells, smooth or with spines.

8. *C. teres.*

Sec. 4. **Compressa** Ostenfeld (93, 1903).

Cells compressed. Terminal setae little different from others. Inner setae of two forms: thinner normal setae, and intercalary thickened and twisted ones. Chromatophores numerous. Resting spores smooth or with a row of spicules.

B. *Each cell with one or two chromatophores.*

Sec. 5. **Protuberantia** Ostenfeld (93, 1903).

Two chromatophores, each with a large pyrenoid situated in a protuberance in the middle of the valve surface. Resting spores with two long horns.

9. *C. didymus.*
10. *C. strictum.*

Sec. 6. **Constricta** Ostenfeld (93, 1903).

Chromatophores one or two. Cells more or less constricted. Girdle at least one-third the length of the cell. Terminal setae mostly thicker than the others. Resting spores about the middle of the cell and with numerous spines on both valves.

11. *C. vanheurckii.*
12. *C. constrictus.*

Sec. 7. **Stenocincta** Ostenfeld (93, 1903).

One chromatophore. Girdle narrow, not one-third the length of the cell. Apertures rather narrow. Terminal setae rather thicker than others, curved and for the most part diverging greatly. Resting spores about the middle of the cell and with numerous spines on both valves.

Sec. 8. **Laciniosa** Ostenfeld (93, 1903).

Chromatophores one or two. Girdle rather long. Apertures rather large. Terminal setae rather thicker than others, not diverging greatly. Resting spores smooth or with minute spines on primary valve, not in the middle of the cell.

Sec. 9. **Diadema** (Ehrenberg) Ostenfeld emen. Gran (47, 1905).

One chromatophore. Chains long with conspicuous terminal setae. Primary valve of resting spore with branched process or crown of spines or sometimes smooth. Occasionally both valves armed.

13. *C. seiracanthus.*
14. *C. subsecundus.*
15. *C. difficile.*

Sec. 10. **Diversa** Ostenfeld (93, 1903).

Short rigid chains. Inner setae of two kinds. Terminal setae less spread out than a special pair of setae in middle of cell. One chromatophore.

16. *C. messanensis.*

Sec. 11. **Brevicatenata** Gran (47, 1905).

One or two chromatophores. Short straight chains, few joints. Terminal setae very thin, more or less different from others. Mostly small to very small forms.

Sec. 12. **Curviseta** Ostenfeld emen. Gran (47, 1905).

One chromatophore. Setae curved, all bent in one direction. Chains usually curved, without special end cells.

17. *C. curvisetus.*

Sec. 13. **Anastomosantia** Ostenfeld (93, 1903).

Setae united by a bridge.

Sec. 14. **Furcellata** Ostenfeld (93, 1903).

One chromatophore. Terminal setae not differentiated. Resting spores excentrically arranged in mother cell, lying close together, two and two, with thick fused setae; with smooth valves or with short spines.

Sec. 15. **Socialia** Ostenfeld (93, 1903).

Chains curved, embedded in mucilage, forming irregular spherical colonies. One chromatophore. Resting spores smooth or with small spines.

18. *C. socialis.*

Sec. 16. **Simplicia** Ostenfeld (93, 1903).

Cells living singly or two or three together.

19. *C. gracilis.*
20. *C. parallelis.*

Sub-genus 1. **PHAEOCEROS.**

Sec. 1. ATLANTICA.

Species 1. **Chaetoceros atlanticum** Cleve (24, 1873*b*, p. 11).

Synonyms:

Chaetoceros dispar Castracane (23, 1886, p. 76), *Chaetoceros audax* Schütt (107, 1895, p. 47), *Chaetoceros polygonum* Schütt (107, 1895, p. 46).

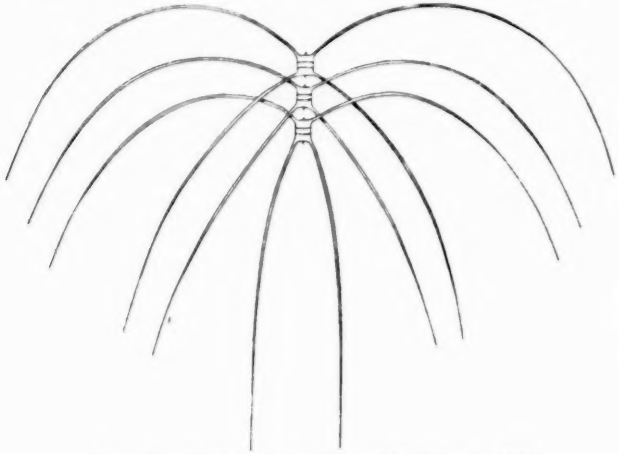

FIG. 47.—*Chaetoceros atlanticus.* After Karsten, 1905.

Chains straight, flat, 15–40 μ broad. Valves elliptical, furnished with small central spine. Apertures hexagonal, large. Setae have narrow base just inside cell corner, thicken suddenly and taper slowly further out. Distinct constriction between low valve mantle and girdle zone. Terminal

setae shorter and thicker than others, directed outward at base and bent towards pervalvar axis further out. Chromatophores numerous, small rounded bodies, penetrating the setae.

Oceanic. Identified in this region by both Hendy and Karsten.

Variety **"neapolitana"** (Schröder) Hustedt (65, 1927, p. 645).

Synonym: *Chaetoceros neapolitanum* Schröder (53, 1900, p. 29).

Cells similar to type but much narrower, 8–12 μ. Valves elliptical, central spine difficult to see. Setae similar to type but run parallel with

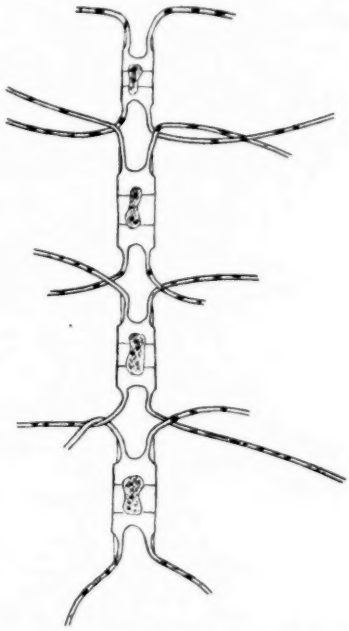

FIG. 48.—*Chaetoceros atlanticus* var. *neapolitana*. Chain in broad girdle view. After Cupp, 1943.

pervalvar axis for short distance before turning outward to cross setae of neighbouring cells. Apertures oblong to diamond-shaped. Chromatophores as in type.

Oceanic, temperate form. Reported by Hendy as occurring frequently in this area.

Sec. 2. Borealia.

Species 2. **Chaetoceros peruvianus** Brightwell
(18, 1856, p. 107).

Synonyms:

Chaetoceros peruvianus var. *currens* Péragallo (97, 1897, pl. 125, f. 2), *C. convexicornis* Mangin (81, 1919, p. 3), *C. peruvianus* var. *currens* Forti (41, 1922, p. 149).

Cells usually solitary, occasionally in short chains. Upper valve rounded, lower flat. Setae of upper valve originate near centre, turn sharply, and run backward in outwardly convex curves. Setae of lower valve originate near margin, outwardly slightly convex, run more parallel with pervalvar axis than those of upper valve. Setae thick and armed with strong spines.

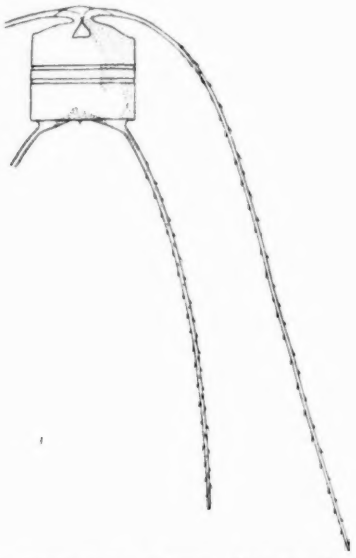

Fig. 49.—*Chaetoceros peruvianus.* Diameter of cell 22 μ.

Species 3. **Chaetoceros convolutum** Castracane
(23, 1886, p. 78).

Synonyms:

Chaetoceros brightwellii Gran (47, 1897, p. 11) (nec Cleve), *Chaetoceros criophilus* Cleve (24, 1901, p. 20).

Cells united in chains 15–30 μ broad, curved or slightly twisted. Valves unequal, upper one arched, lower flat. Valve mantle almost as deep as girdle zone, definite constriction at junction of two. Setae arise at centre of upper valve, at corners of lower, bend toward one end of chain, and are armed with small spines. Chromatophores numerous, small, rounded bodies.

Reported as very common by Hendy.

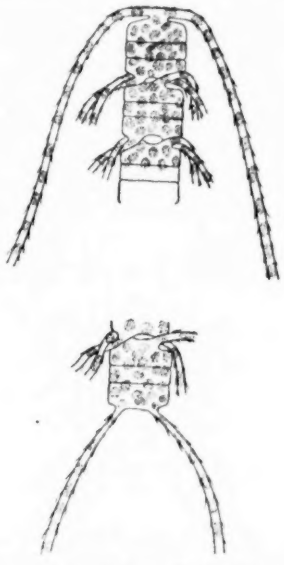

FIG. 50.—*Chaetoceros convolutom.* Chain in broad girdle view. Partly after Gran and Angst, 1931.

Sub-genus 2. **HYALOCHAETE.**

Sec. 1. OCEANICA.

Species 4. **Chaetoceros decipiens** Cleve

(24, 1873*b*, p. 11).

Synonyms:

Chaetoceros concretus Engler (38, 1883, p. 11), *Chaetoceros grunowii* Schütt (107, 1895, p. 43), *Chaetoceros decipiens* f. *singularis* Gran (47, 1904, p. 536).

Cells rectangular in broad girdle view, 10–80 μ broad. Corners of cells touch those of next cell forming long, straight, stiff chains. Apertures

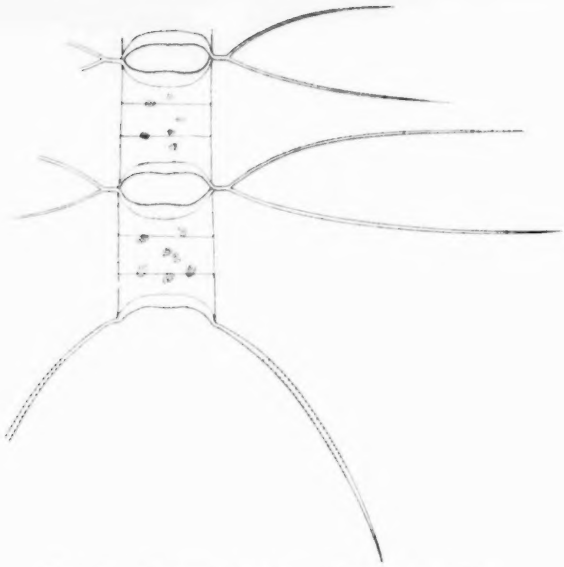

FIG. 51.—*Chaetoceros decipiens*. Diameter of cell 22 μ.

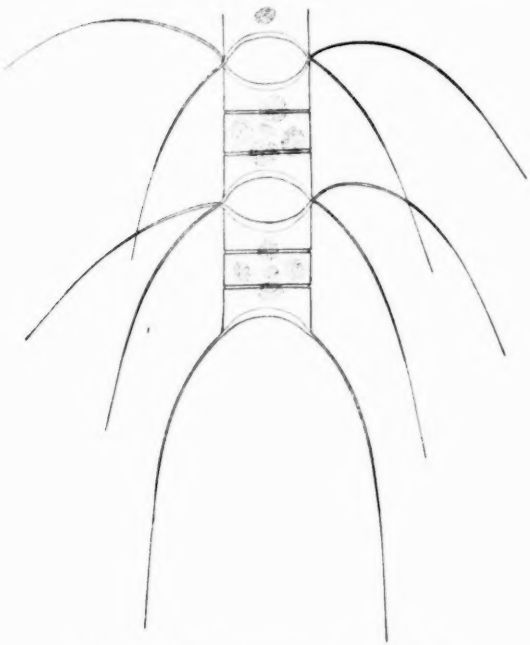

FIG. 52.—*Chaetoceros capense*. Apical axis 13 μ.

vary in size and shape. Setae originate at cell corners, directed perpendicular to chain axis. Fused for a length 2–3 times the diameter of the setae. Terminal setae shorter and thicker, first directed outward and then bending to become nearly parallel with chain axis. Setae have no particular sculpturing. Occasionally heavily punctated like *Chaetoceros lorenzianus*. Chromatophores 4–10 per cell.

Sec. 2. DICLADIA.

Species 5. **Chaetoceros capense** Karsten
(68, 1906, p. 167).

Cells small, valves elliptical, apical axis 10–18 μ. Valve surface concave. Long thin setae originate at corners. United to form chains, 4–8 cells per chain. Valve mantle deep. Sharp constriction at girdle zone. Chromatophores 4 irregular plates.

Species 6. **Chaetoceros lorenzianus** Grunow
(56, 1863, p. 157).

Synonym: *Chaetoceros cellulosum* Lauder (71, 1864, p. 78).

Cells rectangular in girdle view. Apertures polygonal to elliptical. Setae fused only at point of exit from margin, strongly punctate. Terminal setae divergent for entire length. Chromatophores large, plate-like, 4–10 per cell. Diameter of cell 20–50 μ.

Species 7. **Chaetoceros tetras** Karsten
(68, 1905, p. 167).

Form with a high girdle zone, 2–3 times higher than valve, with a slight constriction between valve mantle and girdle zone. Valves similar to each other, slightly concave, with slight convexity in centre. Anterior terminal valve furnished with stronger convexity, posterior terminal valve more strongly concave. Apertures elliptical, narrowed in the centre. Setae slender, short, directed outward. Anterior terminal setae stronger, directed parallel with pervalvar axis. Posterior terminal setae considerably stronger, directed downward. Occasional adjacent pairs of setae, stronger than the others, are also directed downward. Chromatophores usually four, plate-like, each with a pyrenoid. In the young cells of this form there are only two chromatophores, which divide immediately.

Described from Capetown by Karsten.

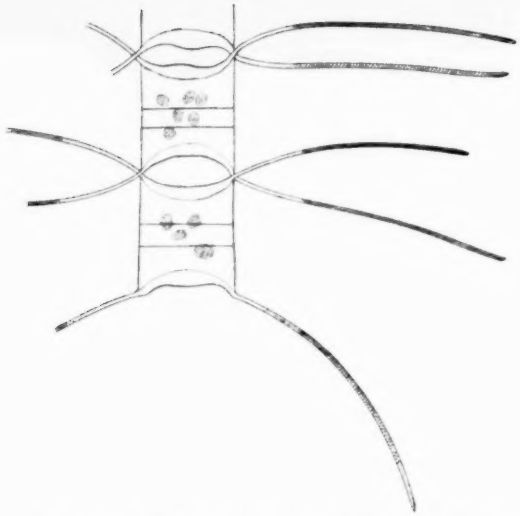

FIG. 53.—*Chaetoceros lorenzianus.* Diameter of cell 31 μ.

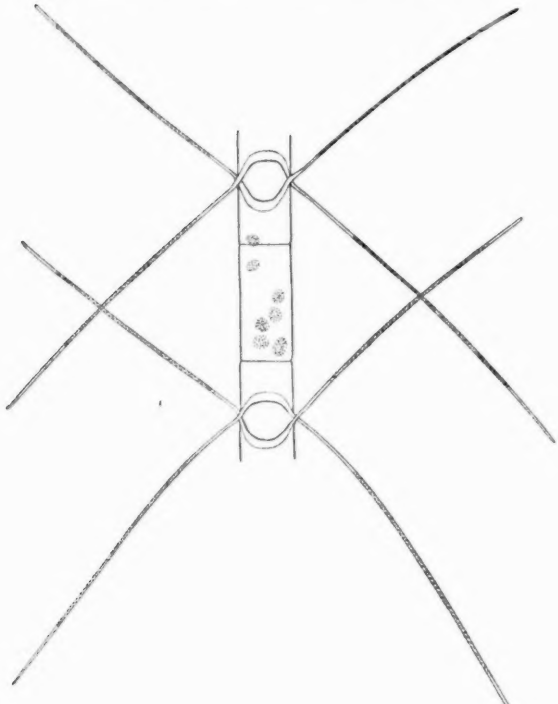

FIG. 54.—*Chaetoceros lorenzianus.* Diameter of cell 12·6 μ.

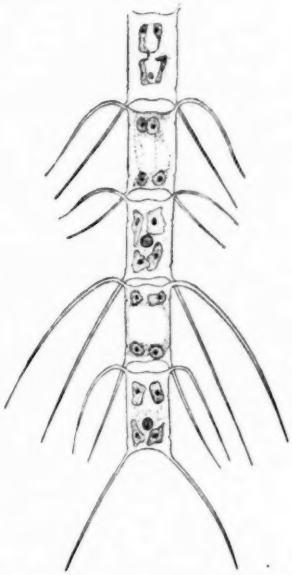

FIG. 55.—*Chaetoceros tetras.* Chain showing cell contents. After Karsten, 1905.

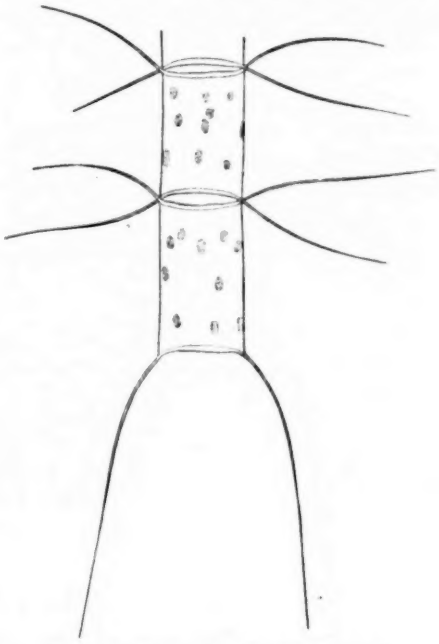

FIG. 56.—*Chaetoceros teres.* Diameter of cell 19·2 μ.

Sec. 3. CYLINDRICA.

Species 8. **Chaetoceros teres** Cleve

(24, 1896*b*, p. 30).

Cells cylindrical, 18–48 μ in diameter. Rectangular in broad girdle view with sharp corners, longer than broad. Apertures very narrow. No constriction between low valve mantle and high girdle zone. Setae originate at cell corners and extend perpendicular to chain axis. Numerous small chromatophores. Numerous intercalary bands invisible in water mounts.

Sec. 5. PROTUBERANTIA.

Species 9. **Chaetoceros didymus** Ehrenberg

(37, 1846, p. 75).

Synonyms:

Goniothecium gastridium Ehrenberg (37, 1845*b*, p. 82), *Chaetoceros gastridium* Ehrenberg (37, 1846, p. 76), *Chaetoceros mamillanum* Cleve (24,

1889, p. 55), *Chaetoceros protuberans* Schütt (5, 1901, p. 41), *Chaetoceros didymus* var. *hiemalis* Tempère and Péragallo (117, 1907), *Chaetoceros didymus* var. *genuina* Gran and Yendo (49, 1914, p. 12).

Chains straight, cells compressed in broad girdle view, with concave end surfaces, and a semicircular knob in the centre. Length of apical axis 10–40 μ. Setae arise at cell corners and cross at base or further out. Two chromatophores per cell, each with a pyrenoid located in the protuberance.

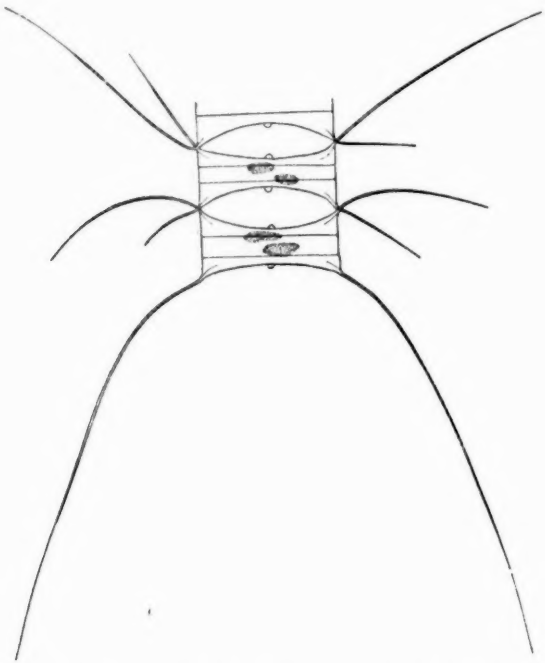

FIG. 57.—*Chaetoceros didymus.* Diameter of cell 21 μ.

Variety **"protuberans"** (Lauder) Gran and Yendo (49, 1914, p. 12).

Synonyms:

Chaetoceros protuberans Lauder (71, 1864, pl. 8, f. 11), *Chaetoceros didymus* Okamura (91, 1907, p. 95).

Similar to type. Terminal setae more strongly divergent than in type,

convex toward outside, usually thicker than other setae. Inner setae usually cross further out than in type.

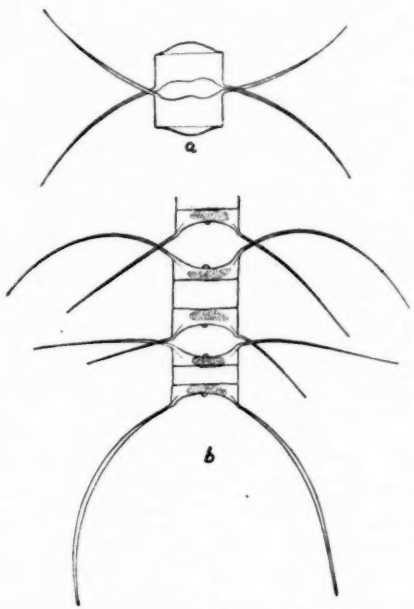

FIG. 58.—*Chaetoceros didymus.* *a.* Resting spore. *b.* var. "*protuberans.*" Diameter of cell 32 μ.

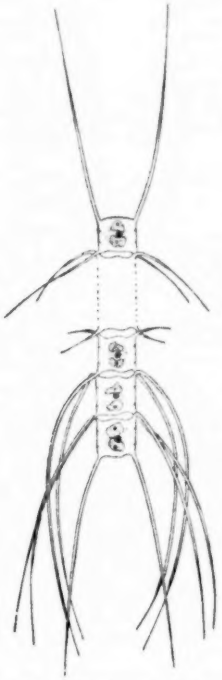

FIG. 59.—*Chaetoceros strictum.* Part of chain with cell contents. Partly after Karsten, 1905.

Species 10. **Chaetoceros strictum** Karsten

(68, 1905, p. 168).

Cells rectangular in broad girdle view, valves similar, elliptical. Slight constriction at junction of valve mantle and girdle zone. Terminal setae at both ends of the colony strongly developed and running parallel with pervalvar axis. The remaining setae are all bent sharply toward the one end. In this formation they vary, some being poorly developed, others bending strongly toward the terminal setae. Two plate-like chromatophores with small pyrenoids.

Described from this area by Karsten.

Sec. 6. CONSTRICTA.

Species 11. **Chaetoceros vanheurckii** Gran
(47, 1897, p. 18).

Synonyms:

Chaetoceros ralfsii van Heurck (119, 1880, pl. 82B/3), *Chaetoceros constrictum* Gran (50, 1930).

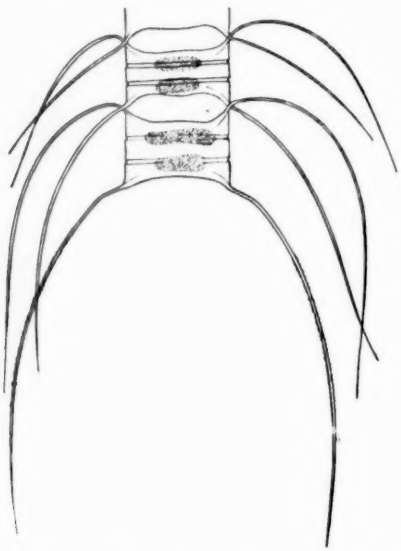

FIG. 60.—*Chaetoceros vanheurckii.* Diameter of cell 18 μ.

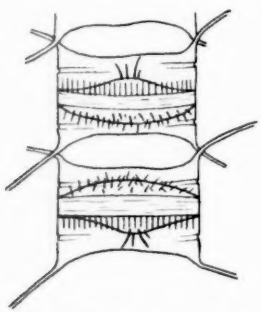

FIG. 61.—*Chaetoceros vanheurckii.* Resting spores.

Cells rectangular in broad girdle view, 14–36 μ broad. United in short chains. Apertures lanceolate. Valves flat to slightly concave. Setae slender. Terminal setae strong with spinules in spirals. Chromatophores two per cell. Resting spores armed with short spines. Set of parallel spines on valve rim.

Species 12. **Chaetoceros constrictus** Gran
(47, 1897*a*, p. 17).

Cells 12–35 μ wide, rectangular in broad girdle view, with sharp corners. Marked constriction between valve and girdle zone. Valves concave, raised slightly in centre. Setae with no basal part. Terminal setae acutely divergent. Chromatophores two per cell.

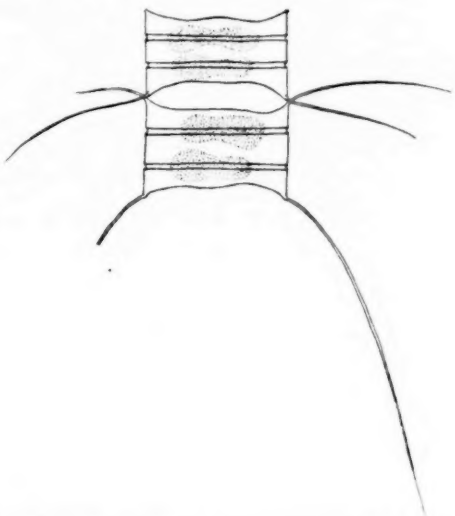

Fig. 62.—*Chaetoceros constrictus.* Diameter of cell 16·5 μ.

Sec. 9. Diadema.

Species 13. **Chaetoceros seiracanthus** Gran
(47, 1897*a*, p. 21).

Cells rectangular in girdle view. Valves fairly flat. Apertures long, oval. One chromatophore per cell, attached to broad side of girdle. Setae arise at cell corners, directed transverse to base. Terminal setae diverge at an acute angle. Diameter of cell 12–24 μ. Both valves of resting spores

armed with unbranched spines. In addition, primary valve has a crown of thin, parallel needles on the margin.

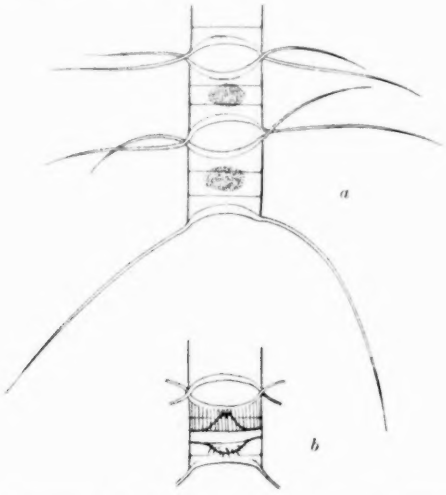

FIG. 63.—*Chaetoceros sciracanthus*. *a*. End of chain. Diameter of cells 17 μ. *b*. Resting spores.

Species 14. **Chaetoceros subsecundus** (Grunow) Hustedt (65, 1927, p. 709).

Synonyms:

Syndendrium diadema Ehrenberg (37, 1854, pl. 34A, f. 18), *Chaetoceros distans* var. *subsecunda* Grunow (119, 1880, pl. 82, B/f. 6), *Chaetoceros paradoxus* var. *lüdersii* Engler (38, 1883, p. 11), *Chaetoceros paradoxus* var. *subsecunda* van Heurck (119, 1880, p. 20), *Chaetoceros curvisetus* Cleve (24, 1894, p. 12), *Chaetoceros paradoxus* Schütt (107, 1895, p. 37), *Chaetoceros clevei* Schütt (107, 1895, p. 40), *Chaetoceros ralfsii* Schütt (107, 1896, p. 53), *Chaetoceros groenlandicus* Cleve (24, 1896*a*, p. 7), *Chaetoceros groenlandicus* var. *leptopus* Cleve (24, 1896*a*, f. 5), *Chaetoceros diadema* Gran (47, 1897*a*, p. 20), *Chaetoceros paradoxus* Péragallo (97, 1897, pl. 132, f. 1).

Cells rectangular in girdle view with weakly rounded corners. Valves flat to slightly convex in centre. Apertures long, oval, narrowing toward middle. Setae originate at cell corners and are directed transversely to chain axis. Terminal setae acutely divergent. One chromatophore per cell. Diameter of cell 12–44 μ. Primary valve of resting spore armed with 4–12 dichotomously branching spines. Secondary valve smooth.

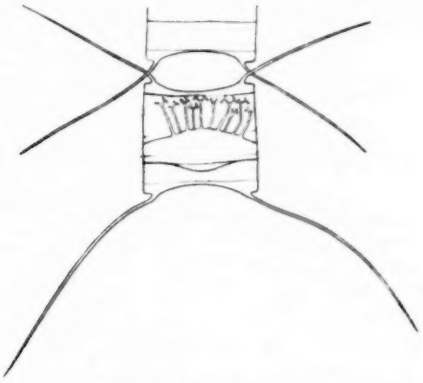

FIG. 64.—*Chaetoceros subsecundus.* Resting spore.

Species 15. **Chaetoceros difficile** Cleve
(24, 1900*a*, p. 20).

Chain straight, loose, 7–15 μ broad. Cell wall weakly siliceous. Valves flat, with no constriction between valve mantle and girdle zone. Setae

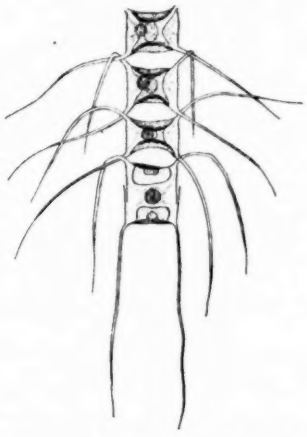

FIG. 65.—*Chaetoceros difficile.* Chain with cell contents. Partly after Karsten, 1905.

very thin, arising at cell corners, with short basal part directed diagonally outward. Apertures wide, hexagonal to rectangular. Chromatophores one per cell attached to broad side of girdle.

Neritic. Reported from Capetown by Karsten as "*Ch.* (*difficile* Cl.?) or a new species". From his short description and figures this would appear to be *Chaetoceros difficile*.

Sec. 10. Diversa.

Species 16. **Chaetoceros messanensis** Castracane

(23, 1875, p. 32).

Synonyms:

Chaetoceros spec. Lauder (71, 1864, pl. 3, f. 8), *Chaetoceros furca* Cleve (24, 1897*a*, pl. 1, f. 10), *Chaetoceros furca* var. *macroceros* Schröder (104, 1906*a*, p. 351), *Chaetoceros cornutus* Leudeger-Fortmorel (75, 1898, p. 8).

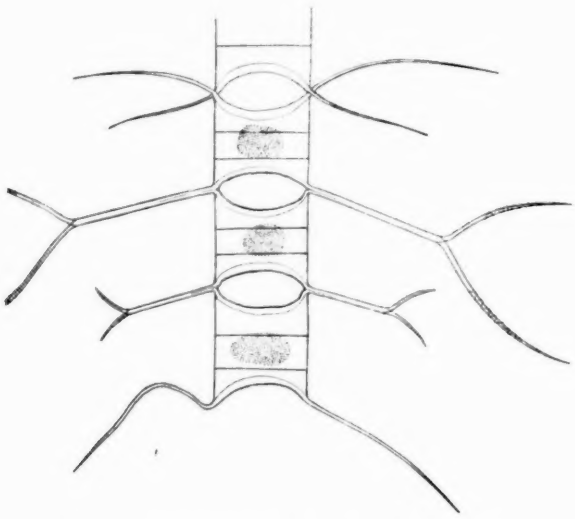

Fig. 66.—*Chaetoceros messanensis*. Diameter of cell 13 μ.

Cells rectangular, corners of adjacent cells touching one another. Diameter of cell 12–14 μ. Chains straight. Valves elliptical. Setae thin. Terminal setae unlike one another, diverging strongly. Some of the inner setae are fused for about two-thirds of their length and then fork. The forked setae are thicker than the others, and armed with spirals of conspicuous small spines. One chromatophore per cell.

Sec. 12. CURVISETA.

Species 17. **Chaetoceros curvisetus** Cleve

(24, 1889, p. 55).

Synonyms:

Chaetoceros spec. Schütt (107, 1889, pl. 14, fs. 1–7), *Chaetoceros secundus* Schütt (107, 1893, p. 25).

Cells rectangular in broad girdle view, with conspicuous corners, elliptical in valve view, apical axis 10–30 μ. Valve mantle low with high corners to apical axis. Chains spirally curved, no distinct terminal cell. Apertures rhombo-elliptical to circular. Setae originate at cell corners and all bend toward outside of curved axis of spiral. Chromatophores large, one per cell, with central pyrenoid.

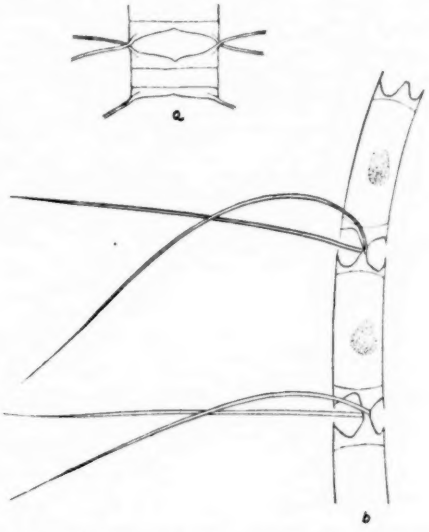

FIG. 67.—*Chaetoceros curvisetus*. *a*. Broad girdle view. *b*. Narrow girdle view.

Sec. 15. SOCIALA.

Species 18. **Chaetoceros socialis** Lauder

(71, 1864, p. 77).

Synonyms:

Chaetoceros wighami Grunow (25, 1880, pl. 7, f. 134), *Chaetoceros lonrezianus* var. *parvula* Grunow (25, 1880, pl. 7, f. 138), *Chaetoceros socialis* var.

solitaria Meunier (84, 1913, p. 46), *Chaetoceros socialis* var. *flabelliformis* Meunier (84, 1913, f. 26), *Chaetoceros socialis* var. *congesta* Meunier (84, 1913).

Cells four-cornered in broad girdle view, corners not touching those of adjacent cell. Width of cell 4·5–15 μ. United into short chains which combine to form colonies. Setae hair-like, originating at cell corners, three short, fourth very long and entwining with long setae of adjacent cells to form colonies. Chromatophores one per cell.

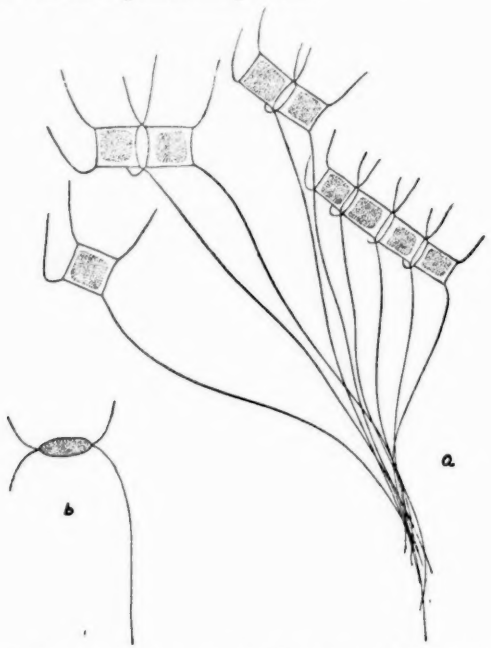

FIG. 68.—*Chaetoceros socialis*. *a*. Part of colony. *b*. Cell in valve view.

Sec. 16. SIMPLICIA.

Species 19. **Chaetoceros gracilis** Schütt (107, 1895, p. 42).

Synonyms:

Eucampia payeri Grunow (56, 1884, p. 107), *Chaetoceros septentrionalis* Cleve (24, 1896*a*, p. 9).

Cells solitary, rectangular in broad girdle view, with conspicuous corners and flat to concave valves, 6–10 μ broad. Setae originate a little within

the corners, curved near origin and later more nearly parallel. Chromatophores two per cell.

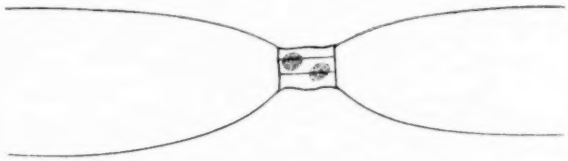

FIG. 69.—*Chaetoceros gracilis.* Apical axis 8·1 μ.

Species 20. **Chaetoceros parallelis** Boden (12, *in press*).

Cells solitary, rectangular in broad girdle view. Valves concave, elliptical in valve view. Valve mantle fairly high, with slight constriction

FIG. 70.—*Chaetoceros parallelis.* Diameter of cell 12·1 μ.

at junction of valve mantle and girdle zone. Slender setae originate at cell corners and run almost parallel with pervalvar axis, slightly convex on outside. Chromatophores numerous cocciform bodies. Width of cell in girdle view 10·8–13·5 μ, length of cell 21·6–28 μ, length of setae 121–135 μ.

The numerous chromatophores of this form make it doubtful whether it belongs in this section.

5. Biddulphiae Schütt.

a. Eucampiinae Schütt.

Genera: I. *Eucampia.*
II. *Climacodium.*
III. *Streptotheca.*

Genus I. **EUCAMPIA** Ehrenberg
(37, 1839, p. 151).

Cells united in spiral chains. Valves elliptical in surface view, with two blunt processes but lacking spines or bristles. Intercalary bands difficult to see. Apertures large. Chromatophores numerous, small.

Species: *E. zoodiacus.*
E. cornuta.

Species 1. **Eucampia zoodiacus** Ehrenberg
(37, 1839, p. 151).

Synonyms:

Eucampia britannica W. Smith (113, 1853, p. 25), *Eucampia nodosa* A. Schmidt (103, 1875, pl. 141, f. 28), *Eucampia zoodiacus* var. *cornigera* Grunow (119, 1880, pl. 95B, f. 4), *Eucampia virginica* Grunow (119, 1880, pl. 95B, f. 6), *Eucampia cornuta* var. ? Cleve (24, 1901*a*, p. 326).

Cells flattened, united in spiral chains by two blunt, valvar processes. Apertures variable. Chromatophores small, numerous. Length along apical axis 10–61 μ.

Species 2. **Eucampia cornuta** (Cleve) Grunow
(119, 1880, pl. 95B, f. 5).

Synonym: *Moelleria cornuta* Cleve (24, 1873*a*, p. 7).

Chain and general appearance similar to Eucampia zoodiacus. Valvar processes longer, thinner. Apertures wider. Intercalary bands more prominent. Sculpturing of valves more noticeable and definite in arrangement.

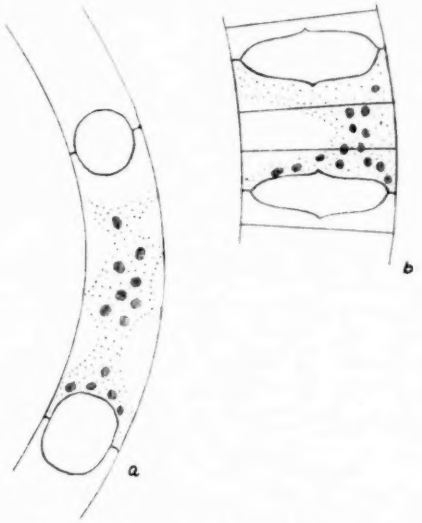

FIG. 71.—*Eucampia zoodiacus*. *a*. Width of chain 22 μ. *b*. Width of chain 39·7 μ.

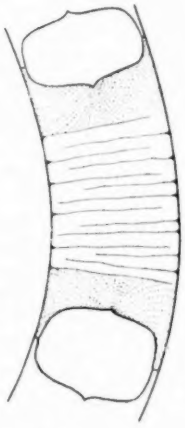

FIG. 72.—*Eucampia cornuta*. Width of cell 13·5 μ. Length of cell 23 μ.

Genus II. **CLIMACODIUM** Grunow

(56, 1868, p. 102).

Chains straight with apertures oval or oblong. Hammer-like ends of cells touch to form chains. Cell walls weakly siliceous. Chromatophores numerous, small.

Species: *C. frauenfeldianum*.

Species 1. **Climacodium frauenfeldianum** Grunow

(56, 1868, p. 102).

Synonyms:

Climacodium (*frauenfeldianum* var. ?) *jacobi* Cleve (24, 1897*a*, p. 22), *Climacodium atlanticum* Mangin (81, 1910, p. 383).

Chains ribbon-like with large rectangular apertures. Pervalvar axis 10–15 μ. Intercalary bands absent. Chromatophores small, numerous.

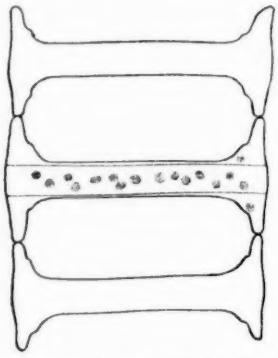

FIG. 73.—*Climacodium frauenfeldianum*. Width of cell 175·5 μ, length 12 μ.

Genus III. **STREPTOTHECA** Shrubsole
(110, 1890, p. 259).

Cells square, flat, forming ribbon-like chains. United by valve faces leaving hardly any aperture. Chains twisted. Cell wall weakly siliceous. Chromatophores numerous, small. Valve surfaces armed with rudimentary central knob.

Species: *S. thamesis.*

Species 1. **Streptotheca thamesis** Shrubsole
(110, 1890, p. 259).

Cells square, flat, twisted through 90°. Valves with two deeply placed knobs, fitting into corresponding depressions on valve surface of adjacent cell. Chromatophores numerous, small rounded plates. Width of cell 60–160 μ.

b. Triceratiinae Schütt.
Genus: I. *Ditylum.*

Genus I. **DITYLUM** Bailey
(8, 1862, p. 352).

Valve three- to four-cornered, with a strong, siliceous, hollow central spine, and a ribbed marginal ridge. Cells elongated, prismatic to cylindrical, usually solitary. Cell walls weakly siliceous. Chromatophores numerous, small.

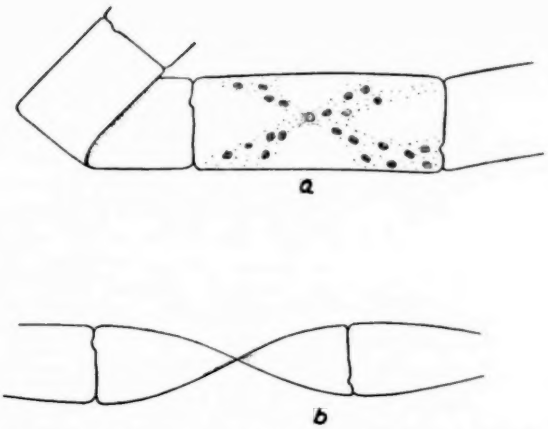

FIG. 74.—*Streptotheca thamesis*. *a*. Part of chain, width 62 μ. *b*. Typical twisting.

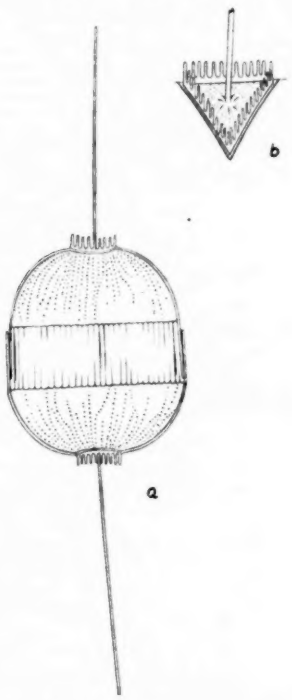

FIG. 75.—*Ditylum brightwellii*. *a*. Diameter of cell 67 μ. *b*. Ridge on valve.

FIG. 76.—*Ditylum brightwellii*. Diameter of cell 35 μ.

Species: *D. brightwellii.*

Species 1. **Ditylum brightwellii** (West) Grunow
(119, 1880, pl. 114, fs. 3–9).

Synonyms:

Triceratium undulatum Brightwell (18, 1858, p. 154), *Triceratium brightwellii* West (121, 1860, p. 149), *Ditylum trigonum* Bailey (8, 1862, p. 332), *Ditylum inaequale* Bailey (8, 1862, pl. 7, fs. 12–14), *Ditylum brightwellii* var. *inaequalis* Grunow (119, 1880, pl. 114, f. 3), *Ditylum brightwellii* var. *trigona* Grunow (119, 1880, pl. 114, f. 9), *Ditylum undulatum* Mann (82, 1907, p. 297).

Cells prism-shaped with strongly rounded angles, to nearly cylindrical. Diameter of cell 25–100 μ. Valves triangular with central hollow spine. Areolae in radial rows on valve surface, in pervalvar rows on valve mantle. Intercalary bands scale-like. Cell wall weakly siliceous. Chromatophores small, numerous.

c. Biddulphiinae Schütt.
Genus: I. *Biddulphia.*

Genus I. **BIDDULPHIA** Gray
(51, 1821, p. 294).

Cells single or in chains, box-shaped to cylindrical. Cell wall strongly siliceous. Valves elliptical to triangular or quadrangular. Strongly developed horns or processes on valves at corners or ends of ellipse. Fine slime pores present at ends of processes. Through these pores appear slime cushions which hold the cells together in chains. In planktonic forms the valves are usually armed with spines. The girdle zone is sharply differentiated from the valve zone, prism-shaped to cylindrical, cross-striated, with indistinct intercalary bands. Chromatophores numerous, small, lying against the cell wall.

Species: *B. mobiliensis.*
B. regia.
B. longicruris.

Species 1. **Biddulphia mobiliensis** Bailey
(7, 1845, p. 336).

Synonyms:

Zygoceros (*Denticella* ?) *mobiliensis* Bailey (7, 1851, p. 40), *Biddulphia baileyi* W. Smith (113, 1853, pl. 45, f. 322*b*), *Denticella mobiliensis* Grunow (56, 1884, p. 7), *Odontella mobiliensis* Grunow (56, 1884, p. 58).

Cells single, sometimes united in short chains by valvar spines. Cell walls relatively thin, weakly siliceous. Valves elliptical, convex, with flat central portion. Valve processes slender, directed diagonally outward. Two long spines directed obliquely outward. The spines are about as far from each other as they are from the valve processes. Sculpturing very fine. Length of apical axis 45–160 μ.

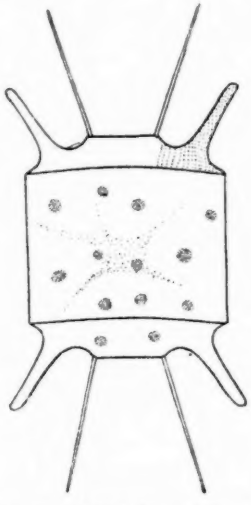

FIG. 77.—*Biddulphia mobiliensis.* Apical axis 94 μ.

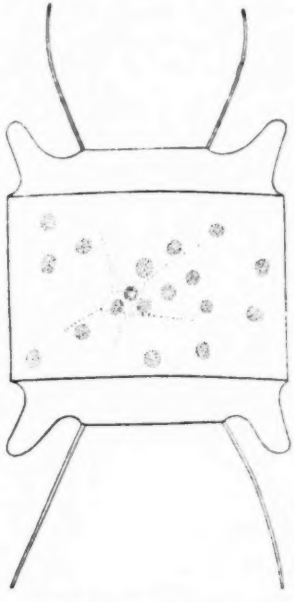

FIG. 78.—*Biddulphia regia.* Apical axis 170 μ.

Species 2. **Biddulphia regia** (Schultze) Ostenfeld (93, 1908*b*, p. 7).

Synonyms:

Denticella regia Schultze (105, 1858, p. 21), *Biddulphia baileyi* W. Smith (113, 1853, pl. 62, f. 322*d*).

Cells similar to, and frequently confused with, *B. mobiliensis*. Central part of valve wider than depressions. Spines further from each other and nearer to processes than *B. mobiliensis*. Processes blunter than *B. mobiliensis*. Length of apical axis 60–180 μ.

Species 3. **Biddulphia longicruris** Greville

(53, 1859, p. 163).

Cells usually in straight chains. Valves elliptical, with a conical protuberance in centre bearing usually two (sometimes three) long spines. Spines usually bent to run more or less parallel with pervalvar axis, capitate-truncate. Valvar processes longer than wide. Valve mantle usually indented above junction with girdle zone. Valves and girdle zone finely punctated. Chromatophores small, numerous, near cell wall. Length of apical axis 15–110 μ.

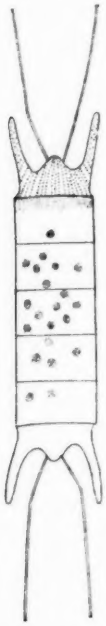

FIG. 79.—*Biddulphia longicruris.* Apical axis 94·5 μ.

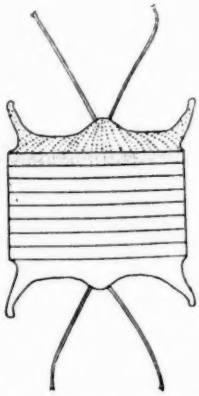

FIG. 80.—*Biddulphia longicruris* var. "*hyalina.*" Apical axis 160 μ.

Variety **"hyalina"** (Schröder) Cupp (30, 1943, p. 157).

Synonyms:

Biddulphia hyalina Schröder (104, 1906*a*, p. 353), *Biddulphia extensa* Mann (82, 1907, p. 302), *Biddulphia longicruris* Greville (48, 1931, p. 491).

Shape of valve similar to type. Spines shorter. Valvar processes shorter, blunter. Intercalary bands usually lacking. Chromatophores numerous, small. Length of apical axis 24–184 μ.

d. Hemiaulinae Schütt.

Genus: I. *Hemiaulus.*

Genus I. **HEMIAULUS** Ehrenberg
(37, 1844, p. 199).

Cells solitary or in chains. Valves elliptical in section, with two processes at ends of apical axis parallel with pervalvar axis. These processes are armed with one or more hyaline claws at the end. Cell wall strongly or weakly siliceous, punctated. Chromatophores numerous.

Species: *H. hauckii.*

Species 1. **Hemiaulus hauckii** Grunow
(119, 1880, pl. 103, f. 10).

Synonym: *Hemiaulus delicatulus* Lemmerman (74, 1905, p. 647).

Cells rectangular in broad girdle view with long, thin, pointed processes uniting them into chains. Apical axis 8–75 μ. Cells long, straight or twisted. Valve surface flat to slightly concave. Apertures large. Cell wall weakly siliceous.

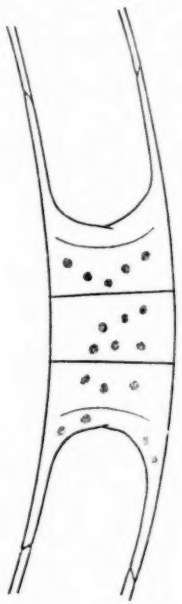

FIG. 81.—*Hemiaulus hauckii.* Apical axis 32 μ.

6. Euodieae Schütt.

Genus: I. *Hemidiscus.*

Genus I. **HEMIDISCUS** Wallich

(120, 1860, p. 42).

Cells cuneiform. Valves semicircular to asymmetrically elliptical. Valves flat with short valve mantles. Cell wall weakly or strongly siliceous, with regular, thick areolation. Marginal spinulae often present, also an "eye" near middle of ventral valve margin. Chromatophores numerous, small bodies.

Species: *H. cuneiformis.*

Species 1. **Hemidiscus cuneiformis** Wallich

(120, 1860, p. 42).

Synonyms:

Dichomeris subtilis Ehrenberg (37, 1861, p. 294), *Euodia inornata* Castracane (23, 1866, p. 149), *Euodia radiata* Castracane (23, 1886, p. 149), *Euodia cuneiformis* Schütt (107, 1896, p. 100), *Euodia gibba*, auct. nonnul., nec Bailey.

Cells cuneiform, solitary. Valves almost semicircular; dorsal margin strongly convex, ventral margin weakly so, often furnished with a median

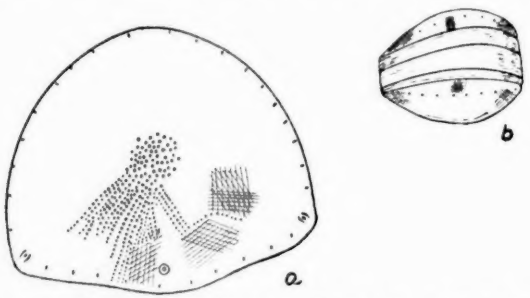

Fig. 82.—*Hemidiscus cuneiformis.* *a.* Valve view. *b.* Girdle view. After Cupp, 1943.

inflation on the ventral side. Valve finely areolated in irregular radial fascicules. No central hyaline area or rosette. Small papillae on apices. Row of small spinulae on ventral margin with small "eye" half-way along. Girdle simple, no intercalary bands. Apical axis 80–174 μ, transapical axis 44–90 μ. Chromatophores numerous, small rounded bodies.

Oceanic. Reported by Hendy, who found the great number of species

and varieties which have been established rely on variable characteristics, and whose specimens formed a "series of intermediate forms that made it impossible to recognise the value of the nomenclatural species and varieties".

CLASSIFICATION OF THE PENNATAE.

B. **PENNATAE** Schütt.

B_1. *Araphideae.*

IV. **Fragilarioideae** Schütt.

7. Tabellaireae Schütt.

a. Licmophorinae Hustedt.

8. Fragilarieae Schütt.

a. Diatominae Schütt.

b. Fragilariinae Schütt.

B_2. *Monoraphideae.*

V. **Acnanthoideae** Schütt.

9. Cocconeideae Schütt.

10. Acnantheae Schütt.

B_3. *Biraphideae.*

VI. **Naviculoideae** Schütt.

11. Naviculeae Schütt.

VII. **Nitzschioideae** Schütt.

12. Nitzschieae Schütt.

VIII. **Surirelloideae** Schütt.

13. Surirelleae Schütt.

KEY TO THE PENNATAE.*

B. Valves not centrally constructed, not arranged in relation to a central point but to a median line. Bilaterally symmetrical. Outline generally boat-shaped or rod-shaped, sometimes oval, cuneate, crescent-shaped, or sigmoid; markings generally pinnate or transverse. True raphe, or hyaline median line (pseudoraphe), or raphe obscured by lateral wings or keel (cryptoraphe) always present. Processes such as horns, spines, etc., uncommon. Cell capable of spontaneous movement if a true raphe is present. Auxospore formation sexual or reduced. Microspores not certainly found . . Section **PENNATAE.**

B_1. Raphe absent. Pseudoraphe usually present . . Subsection **Araphideae.**

IV. Cells in general rod-shaped to tabular-prism-shaped, in valve view usually more or less linear, seldom club-shaped In girdle view linear to tabular-rectangular. Intercalary bands and septa frequently present. Valves with

* Altered from Cupp (1943, p. 36) to fit the Pennate genera of this region.

transapical striae or ribs, sometimes areolated-punctated, often with mucilage pores. Without a true raphe, but usually with a median pseudoraphe. Chromatophores usually more or less numerous small platelets, seldom a single large plate. Auxospore formation, so far as known, asexual . . . Subfamily **Fragilarioideae.**

7. Cells in valve view usually linear, more seldom wedge-shaped, frequently with transapical inflations or constrictions. In girdle view usually linear to tabular, seldom wedge-shaped. Intercalary bands and septa always present and distinct. Valvar plane not bent in the pervalvar direction, the two valves of a cell usually entirely alike. Cells usually united into bands. Marine and freshwater forms . . . . . Tribe **Tabellarieae.**

   (*a*) Cells with poles of apical axis unlike. In girdle view, wedge-shaped. Intercalary bands and septa present. Cells stalked and often united into strongly branched colonies. Marine . . . Subtribe **Licmophorinae.**
   Genus: *Licmophora.*

8. Cells usually rod-shaped. Usually linear in both valve and girdle view, seldom wedge-shaped or with tabular girdle view. Intercalary bands sometimes present, but always without or with only very rudimentary septa . . . Tribe **Fragilarieae.**

   (*a*) Valves with transapical ribs that are, however, sometimes limited to one valve of a cell or to one single middle rib. Freshwater or marine forms. Cells as a rule united into closed or zigzag bands . . Subtribe **Diatominae.**
   Genus: *Plagiogramma.*

(*b*) Valves without special transapical ribs, or the entire membrane provided with a supporting framework of stronger or weaker ribs. Freshwater and marine forms. Cells solitary or united into colonies of various forms. . Subtribe **Fragilariinae.**

Genera: *Fragilaria.*
Thalassionema.
Thalassiothrix.
Asterionella.

B_2. One valve of the cell always with Navicula-like raphe, the other without or with a rudimentary raphe-knot . . . . . Subsection **Monoraphideae.**

V. Cells with linear, lanceolate, or elliptical valvar plane, more or less distinctly bent about the apical or transapical axis. Intercalary bands and septa absent; valves, however, sometimes with polar pseudosepta, individual species also with an intercalary ring with rudimentary chamber-formation on the valve margin similar to the septa-chambers in the genus *Mastogloia*. Structure of the membrane: transapical rows of more or less delicate poroids, often in quincunx. The membrane lying between the transapical rows stronger, often thickened, rib-like. The two valves of a cell often considerably differentiated in regard to the structure as well as to the development of the raphe Subfamily **Acnanthoideae.**

9. Valves isobilateral upon both apical and transapical axes . Tribe **Cocconeideae.**

Genus: *Cocconeis.*

10. Cells bent about the transapical axis, sometimes also about the apical axis; the valve with the raphe, concave; the one without a raphe, convex. One valve always with a developed raphe, the other without, seldom with a very short raphe-knot or with a rudimentary raphe. Outline of valve linear-lanceolate, seldom elliptical. Intercalary bands sometimes present, true septa absent . Tribe **Acnantheae.**

Genus: *Acnanthes.*

B_3. Both valves with developed raphe . . . . Subsection **Biraphideae.**

VI. Cells of various types as regards structure of membrane, cell contents, and general form. All forms with a similar characteristic raphe system: an outer and inner fissure and accompanying end and central knots. Knots often greatly reduced or in many species only slightly developed. Inner and outer fissure often difficult to distinguish from each other. Raphe usually in the valvar plane, generally distinct, not developed as a canal-raphe; usually without a keel or strongly developed wings, but when present always without marginal canal and keel puncta . . . . . Subfamily **Naviculoideae.**

11. Cells as a rule of symmetrical construction, transapical axis only seldom with unlike ends. In girdle view usually rectangular, valves elliptical, linear or lanceolate, often **S**-shaped, seldom club-shaped or crescent-shaped. Raphe usually in the valvar plane. Not perceptibly keeled. Keels if present not punctate. Intercalary bands and septa sometimes present, usually absent. Cells usually solitary, sometimes in gelatinous tubes or on a gelatinous stalk, seldom united into bands and then often difficult to distinguish from *Fragilaria* . Tribe **Naviculeae.**

Genus: *Pleurosigma.*

VII. Keel with canal-raphe lying in the valvar plane, often displaced transapically as far as to the valve margin. In this latter case only one margin of each valve with a keel. Both valves with canal-raphe. Keel with puncta . . . Subfamily **Nitzschioideae.**

12. Raphe obscured by punctate marginal keel. Markings always transverse . . . . Tribe **Nitzscheae.**

Genus: *Nitzschia.*

VIII. Keel with canal-raphe lying on the valve margin and running around the entire valve. Raphe system consequently apparently doubled. Raphe hidden in lateral winged keel . . . . Subfamily **Surirelloideae.**

13. As above . . . . . Tribe **Surirelleae.**

Genus: *Campylodiscus.*

SYSTEMATIC ACCOUNT OF THE PENNATAE.

B. **PENNATAE.**

IV. **Fragilarioideae.**

7. TABELLARIEAE.

a. Licmophorinae Hustedt.
Genus: I. *Licmophora.*

Genus I. **LICMOPHORA** Agardh
(1, 1830, p. 628).

Cells wedge-shaped in girdle view, frequently attached by mucous stalks to living plankton, *e.g.* copepods, or suspended organic matter. Valves wedge- or club-shaped, cross-striated, pseudoraphe distinct. Intercalary bands present with a penetrating septum on upper end. Chromatophores few to numerous, large to small.

Species: *L. ehrenbergii.*
L. lyngbyei.

Species 1. **Licmophora ehrenbergii** (Kützing) Grunow
(56, 1867, p. 36).

Synonyms:

Podosphenia ehrenbergii Kützing (70, 1844, p. 121), *Podosphenia cuneata* Ehrenberg (37, 1838, pl. 17, f. 8).

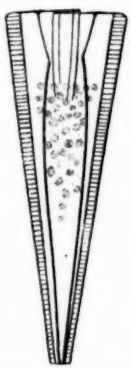

FIG. 83.—*Licmophora ehrenbergii.* Cell in girdle view, length 86·4 μ, width 24·3 μ, striae 9 in 10 μ.

Cells in girdle view wedge-shaped with rounded upper corners. In valve view superior apex rather acute, pseudoraphe broad and distinct, strong clear striations 8–11 in 10 μ. Length of cell 60–180 μ, width 15–30 μ. Chromatophores granular.

Species 2. **Licmophora lyngbyei** (Kützing) Grunow

(56, 1867, p. 35).

Synonym: *Podosphenia lyngbyei* Kützing (70, 1844, p. 121).

Cells united in colonies by means of dichotomously branching mucous stipes. Cells in girdle view three-cornered with both upper corners rounded, clavate in valve view with broad end rounded. Valves flat, transversely striated (10–16 striae in 10 μ), and furnished with a prominent pseudoraphe. Connective zone cuneate, septate. Chromatophores numerous, cocciform bodies. Length of valve 54–80 μ.

Neritic and littoral, frequently epiphytic and epizootic. Reported from this area by Karsten.

FIG. 84.—*Licmophora lyngbyei*. After Wilson in Lebour, 1930.

8. FRAGILARIEAE Schütt.

a. Diatominae Schütt.

Genus: I. *Plagiogramma*.

Genus I. **PLAGIOGRAMMA** Greville

(53, 1859*c*, p. 207).

Cells more or less rectangular in girdle view, lacking intercalary bands or septa. Valves linear-lanceolate, with transapical ribs forming pseudo-

septa. Sometimes two pairs of ribs present, one near centre of valve and one near end; sometimes several pairs of ribs present; sometimes only one rib in centre. Cell wall with delicate transapical and longitudinal ribs. Puncta and areolae in regular longitudinal rows. Cells form close chains.

Species: *P. vanheurckii.*

Species 1. **Plagiogramma vanheurckii** Grunow
(119, 1880, p. 145).

Cells rectangular in girdle view, but constricted below the poles, forming a lanceolate middle part with knob-like corners. Valves lanceolate, 15–45 μ long, 4–5 μ broad. Valve centre has single deeply penetrating pseudoseptum. Transapical and longitudinal striations 12–16 in 10 μ.

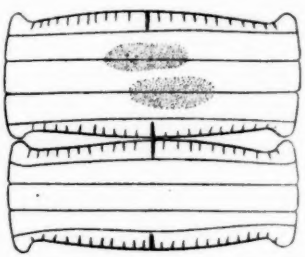

Fig. 85.—*Plagiogramma vanheurckii.* Length of cell 27 μ.

b. Fragilariinae Schütt.

Genera: I. *Fragilaria.*
II. *Thalassionema.*
III. *Thalassiothrix.*
IV. *Asterionella.*

Genus I. **FRAGILARIA** Lyngbye
(80, 1819, p. 182).

Cells in girdle view rectangular and rod-like. United by whole valve surface into ribbon-like chains. Valves linear to elliptical-lanceolate or enlarged or constricted in centre. Valves flat, transapically striated, bilaterally symmetrical, lacking or with rudimentary pseudoraphe, lacking raphe.

Species: *F. granulata.*
F. karstenii.

Species 1. **Fragilaria granulata** Karsten
(68, 1907, p. 396).

Cells united by valve surfaces to form short, curved chains. Valves linear-lanceolate, transversely striated. Length 40–56 μ. Chromatophores numerous, rounded granules.

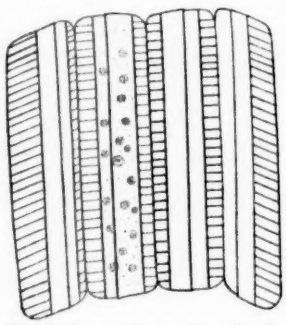

FIG. 86.—*Fragilaria granulata.* Length of cell 48·6 μ.

Species 2. **Fragilaria karstenii** Boden, nom. nov.

Synonym: *Fragilaria capensis* Karsten (68, 1905, p. 173).

42 μ. Valve form? Cells in long bands, valve to valve, rendering it difficult to obtain a valve view. In girdle view one distinguishes 12 to 14 transverse striae on the valve margin. Chromatophores here number four.

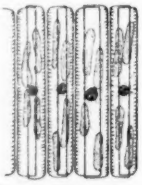

FIG. 87.—*Fragilaria karstenii.* Four cells in girdle view showing cell contents. After Karsten, 1905.

The new name given above is necessary because *Fragilaria capensis* is preoccupied (*F. capensis* Grunow, 1863, p. 143). In the Mill's Index (74, 1933, p. 725) *F. capensis* Karsten is indicated as a synonym for *F. capensis* Grunow. The above description is Karsten's. This form differs from *F. capensis* Grunow in that the cells are united in long bands, the cells are 42 μ long, and the transverse striae are only 3 in 10 μ. *F. capensis*

Grunow is diagnosed by its extremely short bands, by its cells being only 15 to 25 μ long and having 14 to 16 striae in 10 μ. The two forms are therefore different and Karsten's term constitutes a primary homonym and must be replaced. The diagram given by Karsten is reproduced here although it does not agree in all respects with his description.

Genus II. **THALASSIONEMA** Grunow ex Hustedt (65, 1927, p. 244).

Cells linear in girdle view. Valves linear to lanceolate, united by gelatinous cushion at one end into zigzag or star-shaped colonies. Intercalary bands and septa lacking. Numerous, regularly spaced, small spines on valve margins. Chromatophores numerous, small granules. The authority for this genus is attributed to Hustedt by Hendy (1937).

Species: *T. nitzschioides.*

Species 1. **Thalassionema nitzschioides** Hustedt (65, 1932, p. 244).

Synonyms:

Synedra nitzschioides Grunow (56, 1862, p. 403), *Thalassiothrix nitzschioides* Grunow (119, 1880, pl. 43, fs. 7–10), *Thalassiothrix curvata*

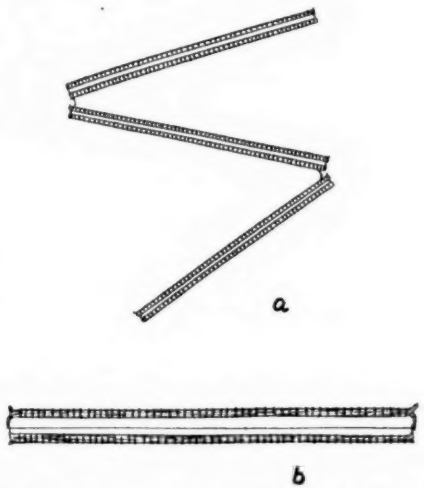

FIG. 88.—*Thalassionema nitzschioides.* *a.* Zigzag colony. *b.* Cell in girdle view, length 48·6 μ, width 3·8 μ.

Castracane (23, 1880, p. 55), *Thalassiothrix frauenfeldii* Cleve (24, 1894, p. 6), *Thalassiothrix frauenfeldii* var. *nitzschioides* Jørgensen (67, 1900, p. 21).

Cells linear in girdle view, narrow. Valves narrow, linear with bluntly rounded ends, 30–110 μ long, 2–4 μ broad. Marginal spines small, 10–12 in 10 μ. Colonies zigzag or star-shaped.

Genus III. **THALASSIOTHRIX** Cleve and Grunow
(25, 1880, p. 108).

Cells narrow, linear in girdle view, solitary or forming zigzag or star-shaped colonies. Valves linear to slightly lanceolate, ends dissimilar. Intercalary bands and septa lacking. Valve margins often armed with small spines. Chromatophores numerous, small granules.

Species: *T. longissima.*

Species 1. **Thalassiothrix longissima** Cleve and Grunow
(25, 1880, p. 108).

Synonym: *Synedra thalassiothrix* Cleve (24, 1873*b*, p. 22.)

Cells solitary, thread-like, curved. Valves narrow linear, one end more narrowed than other. Length 1–4 mm., width 3–4 μ. Valve margin armed with delicate spines, about 3 in 10 μ in centre, fewer or lacking at ends.

Genus IV. **ASTERIONELLA** Hassal
(59, 1855, p. 10).

Cells rod-like with distinctly dissimilar ends, united by larger end into star-shaped, spirally curved, or straight colonies. Valves linear with enlarged area near one or both ends, striated, with narrow pseudoraphe. Intercalary bands and septa lacking.

Species: *A. japonica.*

Species 1. **Asterionella japonica** Cleve and Möller
(27, 1878, No. 307).

Synonyms:

Asterionella glacialis Castracane (23, 1886, p. 50), *Asterionella spathulifera* Cleve (24, 1897*c*, p. 101).

Cells in star-like spiral colonies. In girdle view narrow, linear, with one end enlarged. Length of valve 50–100 μ. Transapical striae 34 in 10 μ. Chromatophores 1 or 2 small plates confined to enlarged end.

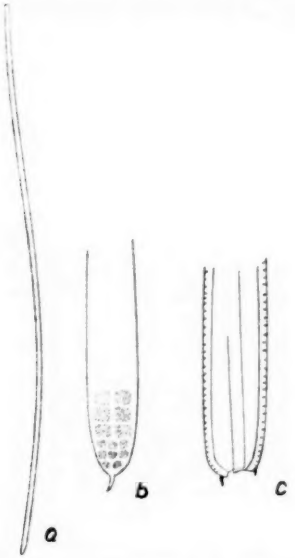

FIG. 89.—*Thalassiothrix longissima*. *a*. Entire cell, length 1 mm. *b*. End of cell, valve view. *c*. End of cell, girdle view.

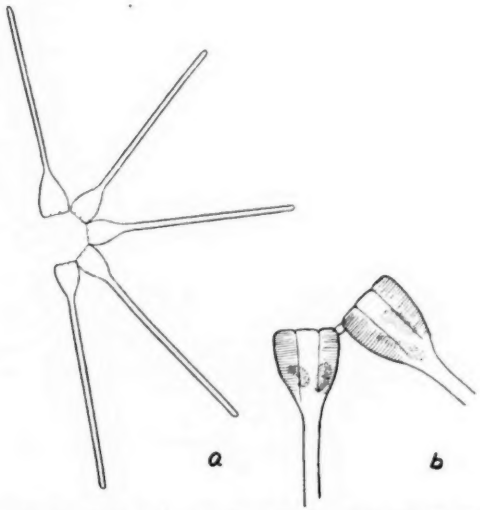

FIG. 90.—*Asterionella japonica*. *a*. Part of colony. *b*. Heads of two cells.

V. **Acnanthoideae** Schütt.

9. Cocconeideae Schütt.

Genus: I. *Cocconeis.*

Genus I. **COCCONEIS** Ehrenberg

(37, 1838, p. 193).

Valves broadly elliptical. Upper valve with more or less narrow longitudinal area. Valve punctated in transverse and, frequently, longitudinal rows. Lower valve usually with marginal area. Valves usually bent along longitudinal axis.

Species: *C. costata.*

Species 1. **Cocconeis costata** Gregory

(52, 1855, p. 39).

Synonyms:

Surirella quarnerensis Grunow (56, 1862, p. 456), *Rhaphoneis scutelloides* Grunow (56, 1862, p. 393), *Cocconeis costata* var. *typica* Cleve (24, 1894–95, p. 182).

Elliptical to orbicular. Upper valve with narrow axial area and strong transverse costae alternating with double rows of puncta. Lower valve with narrow axial area, with central area dilated to a fascia. Cells 12–40 μ long, 8–18 μ broad. Radial transapical striae 6–10 in 10 μ.

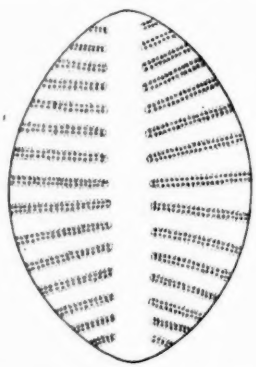

Fig. 91.—*Cocconeis costata.* Upper valve, length 13·5 μ, width 8 μ, striae 10 in 10 μ.

10. ACNANTHEAE Schütt.

Genus: I. *Acnanthes.*

Genus I. **ACNANTHES** Bory

(13, 1822).

Cells solitary or united into ribbon-like chains, with or without a mucous stalk. Valves lanceolate or elliptical. One valve has a raphe and central nodule, the other a pseudoraphe. More or less distinct, transapical striae.

Species: *A. vanhoeffenii.*

Species 1. **Acnanthes vanhoeffenii** Heiden and Kolbe

(61, 1928, p. 580).

Valves lanceolate, length 30–46 μ, width 10–12 μ, radiate striae 10 in 10 μ, wider in mid-portion, 8·5 in 10 μ. Both valves have narrow, lanceolate axial area. Central area of upper valve is asymmetrical due to a shortening of the transapical striae of one side. Narrow lanceolate pseudoraphe on lower valve.

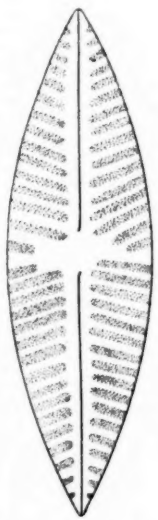

FIG. 92.—*Acnanthes vanhoeffenii.* Upper valve, length 33 μ, width 10·8 μ, striae 10 in 10 μ.

VI. **Naviculoideae** Schütt.

11. Naviculeae Schütt.

Genera: I. *Diploneis.*

II. *Pleurosigma.*

Genus I. **DIPLONEIS** Ehrenberg em. Cleve

(24, 1894–95, p. 96).

Valves usually short, ends rounded, constricted or not in middle. Central nodule prolonged into horns or processes enclosing the median line. On both sides of the horns are furrows of varying width. Fine transverse striae or coarser costae continue in rudimentary state across furrows. The transverse costae are either crossed by longitudinal costae, giving the valve a reticulate appearance, or they alternate with rows of fine puncta or alveoli.

Species: *D. smithii.*

Species 1. **Diploneis smithii** (Brébisson) Cleve

(24, 1894–95, p. 96).

Synonyms:

Navicula elliptica W. Smith (113, 1853, p. 48), *Navicula smithii* Brébisson (113, 1853, p. 92), *Pinnularia scutellum* O'Meara (92, 1875, p. 382), *Navicula smithii* var. *borealis* f. *minor* Grunow (56, 1884, pl. 1, f. 41), *Navicula smithii* var. *scutellum* O'Meara (119, 1886, p. 198), *Navicula gyrinida* Mann (82, 1907, p. 344), *Diploneis gyrinida* Mills (85, 1933, p. 618).

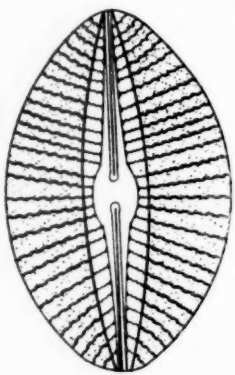

Fig. 93.—*Diploneis smithii.* Length 27 μ, width 15·5μ, striae 12 in 10 μ.

Valve elliptical, 25–200 μ long, 15–75 μ broad. Central nodule small to fairly large. Terminal nodules close to end. Furrows close to horns, of varying width. Transapical striae robust, 5–12 in 10 μ.

Genus II. **PLEUROSIGMA** W. Smith

(113, 1852, p. 1).

Cells elongated, linear to lanceolate, usually sigmoid. Striae punctate, arranged in oblique and transverse or oblique and longitudinal rows. Central area small. Narrow connective zone, cells sometimes twisted or constricted in the middle. Chromatophores usually two bands, one to each valve, with numerous pyrenoids.

Gran (1905) and Lebour (1930) use the generic term "*Gyrosigma*" (Hassal, 1845) as equal to *Pleurosigma*. Cleve (1894), Hustedt (1930), and Cupp (1943) separate *Pleurosigma* and *Gyrosigma* and place in *Pleurosigma* those forms in which the striations in the apical axis are crossed by oblique striations, while *Gyrosigma* designates those forms in which the longitudinal striations cross the transverse striations at right angles. Hendy (1937), considering this did not warrant generic distinction, lumped the two divisions under the title *Pleurosigma* W. Smith, using it in the sense that W. Smith used it in 1852. The one species recorded here belongs to the genus *Pleurosigma* whether the name is used in the restricted or broader sense.

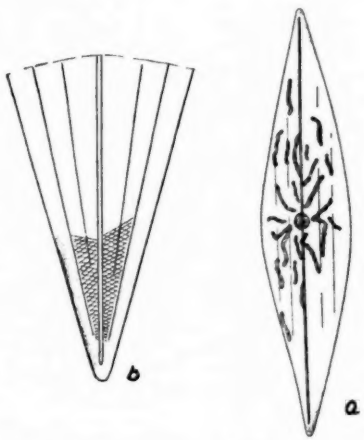

FIG. 94.—*Pleurosigma capense*. *a*. Valve view. *b*. End of cell. After Karsten, 1905.

Species: *P. capense.*

Species 1. **Pleurosigma capense** Karsten
(68, 1905, p. 175).

The valves show the conventional decussate marking in parallel striae running in three different directions, about 20 in 10 μ. Moreover, three of the lines almost parallel with the raphe run on either side of the midline at regular intervals. This is peculiar to this form. Length 320 μ. Chromatophores short bands or rods, radiating from the nucleus in systrophe or arranged on valve surfaces.

Described from here by Karsten.

VII. **Nitzschioideae** Schütt.

12. Nitzschieae Schütt.

Genus: I. *Nitzschia.*

Genus I. **NITZSCHIA** Hassal em. Grunow
(25, 1880, p. 103).

Cells spindle-shaped, single or colonial. Valve keeled, possessing raphe but lacking central nodule. Keels of valves diagonally opposite. Transverse punctate striations. Chromatophores two, band-like.

Species: *N. seriata.*
N. longissima.
N. paradoxa.
N. delicatissima.
N. closterium.

Key to Species.

A. Cells solitary.
  B. Ends hair-like, flexible . . . . . *N. closterium.*
  C. Ends extended into very long horns . . . . *N. longissima.*

A_1. Cells in chain-like colonies.
  D. Chain straight.
    E. Cells large, 6 μ wide . . . . . *N. seriata.*
    F. Cells delicate, 2 μ wide . . . . . *N. delicatissima.*
  D_1. Chain variable in form with the movement of the cells within it . . . . . *N. paradoxa.*

Species 1. **Nitzschia seriata** Cleve
(24, 1883*a*, p. 478).

Synonyms:

Synedra holsatiae Hensen (63, 1887, p. 91), *Nitzschia fraudulenta* Cleve (24, 1897*b*, p. 300).

Cells spindle-shaped, pointed to rounded ends. United into stiff, hair-like chains by overlapping points of cells. Length of valve 80–140 μ, width 6–8 μ. Striations 14–19 in 10 μ, punctate.

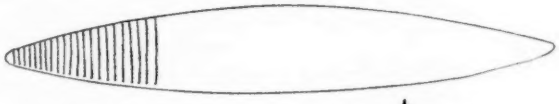

FIG. 95.—*Nitzschia seriata*. *a*. Chain of three cells. *b*. Single cell, valve view. Length 102 μ, width 7 μ, striae 15 in 10 μ.

Species 2. **Nitzschia longissima** (Brébisson) Ralfs
(100, 1861, p. 783).

Synonyms:

Ceratoneis longissima Brébisson (70, 1849, p. 891), *Nitzschia birostrata* W. Smith (113, 1853, p. 42).

Cells solitary. Valves linear-lanceolate, ends extended into long horns. Length 125–250 μ. Chromatophores confined to widened centre. Striations and puncta very difficult to see. About 16 striae in 10 μ.

Species 3. **Nitzschia paradoxa** (Gmelin) Grunow
(119, 1880, p. 176).

Synonym: *Bacillaria paradoxa* Gmelin (77, 1788, p. 3903).

Cells slide along each other, united in movable colonies. Cells 80–250 μ long, 5–6 μ broad, rectangular in girdle view, linear-lanceolate in valve view.

Species 4. **Nitzschia delicatissima** Cleve
(24, 1897*a*, pl. 2, f. 22).

Chains very similar to *Nitzschia seriata*, but much more slender. Length of cell 32–85 μ, width 1·5–2·5 μ. Keels slightly excentric. Puncta 14–25 in 10 μ. No striations visible.

Species 5. **Nitzschia closterium** (Ehrenberg) W. Smith (113, 1853, p. 42).

Synonym: *Ceratoneis closterium* Ehrenberg (37, 1841, p. 64).

Cells single, motile, slightly bent. Ends hair-like. Centre lanceolate, containing a central nucleus and two chromatophores. Length of cell 25–100 μ. Keel puncta about 7 in 10 μ.

Reported by Karsten. Met with frequently in the plankton.

FIG. 96.—*Nitzschia longissima.* Single cell, length 195 μ.

FIG. 97.—*Nitzschia paradoxa.* Valve view, length 82 μ, width 5·2 μ.

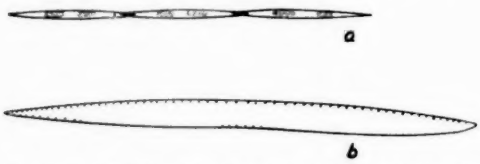

FIG. 98.—*Nitzschia delicatissima.* *a.* Chain of three cells. *b.* Cell in girdle view, length 35·1 μ.

FIG. 99.—*Nitzschia closterium.* Cell 86 μ long. After Cupp, 1943.

VIII. **Surirelloideae** Schütt.

13. SURIRELLEAE Schütt.

Genus: I. *Campylodiscus.*

Genus I. **CAMPYLODISCUS** Ehrenberg

(37, 1841, p. 207).

Valves solitary, saddle-shaped. Valves with a longitudinal central pseudoraphe, that of one valve at right angles to that of the other. Canal pores distinct, usually in parallel rows. Bottom and littoral forms, occasionally found in the plankton.

Species: *C. ralfsii.*

Species 1. **Campylodiscus ralfsii** W. Smith

(113, 1853, p. 30).

Valves nearly circular; canaliculi reaching to the median line. Diameter 40·7 μ to 48·3 μ.

Littoral. Occurs frequently in the plankton.

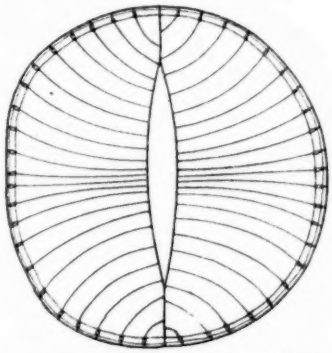

FIG. 100.—*Campylodiscus ralfsii.* Valve view.

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THE PLACENTATION OF *ELEPHANTULUS*.*

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(With seventy-one Text-figures.)

(Read June 15, 1949)

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INTRODUCTION.

To begin with, the following statement has to be made.

Some fifteen years ago I began collecting and preparing the extensive material required for this study on the placentation of *Elephantulus*. During the last three or four years I was greatly assisted by Dr. J. Gillman in the actual research work, and it was the intention to publish the results under both our names, in the same way as we had studied and reported upon several aspects of the reproductive phenomena of *Elephantulus* before. Dr. Gillman, however, became so much occupied with other important work that he could not devote as much time and energy to this study as was necessary for the progress and the conclusion of the work. I therefore, with the consent of Dr. Gillman, have finished it alone. At the time our collaboration came to an end the descriptive part had been written; since that time it has been thoroughly revised, some sections have been rearranged, others rewritten. I alone, therefore, am responsible for any omissions and possible mistakes that still may be found in it. The Discussion, as well as this Introduction, were written by me. Some of the ideas laid down in this work may have originated in Dr. Gillman's mind, but as we had so many discussions and disputes on different aspects of the subject in the course of several years, the precise origin of each idea is quite lost; moreover, the final conclusions may be totally different from the original conceptions. I wish to express my sincere thanks to Dr. Gillman for his co-operation.

Having published several shorter articles on various aspects of the reproduction of *Elephantulus*, the intricate question of the placentation deserved careful attention. When studying the formation and the structure of the placenta, it became evident that this question could not be dissociated from other phenomena taking place in the uterus during pregnancy. The changes in the uterine wall, the decidual reaction, the uterine glands and blood-vessels, as well as the external form of the uterus, are all intimately connected with the development of the placenta. The embryonic membranes also had to be considered. Of course, the embryo itself is closely associated with all events that proceed around it during its development and, therefore,

an account of this development should have been included in order to co-ordinate it with the placental development. This has not been done, because the necessary data are as yet not available; this study in itself would have been an enormous task. The early development was described in two previous papers (van der Horst, 1942 *a*, 1944 *a*), and a detailed study of the *Elephantulus* embryo during the somites stages by Miss C. Gilbert is nearly ready for publication. Even so, as will be explained below, the developmental stage of the embryo at any given moment proved to be the only available means of timing the succeeding events.

Although several species of *Elephantulus* and of the nearly related genera *Macroscelides*, *Nasilio* and *Petrodromus*, all belonging to the family Macroscelididae, occur in South Africa, and material of some of these species was available or might have been obtained, this study was restricted to a single species, *Elephantulus myurus jamesoni* (Chubb, 1909). So whenever in the following pages the name *Elephantulus* is used, it refers to this species only. Differences between the species may occur (van der Horst, 1944 *b*); a more detailed analysis of these differences may form the object of some future study. Some sections of the placenta of *Nasilio*, presented to me by Professor Gérard, show exactly the same picture as is seen in *Elephantulus* and, as far as is known at present, all Macroscelididae have the same type of placenta.

Elephantulus myurus jamesoni is an animal not infrequently seen at suitable places on the Transvaal Highveld, provided one knows where to look for it. To catch the animals alive is another problem, as they take refuge under boulders and large stones at any approaching danger. A special technique for catching the animals had to be devised first; this gave satisfactory results and, once an animal had been located, it had not much chance of escaping. Even so, a day's collecting rarely yields more than a dozen animals, of which, at the appropriate time of the year, three or four may be suitable from an embryologist's point of view. It has taken about ten years to assemble the collection used for this study. I hope that the following pages will show that it was worth the trouble.

Elephantulus can be kept in captivity for a long time, considering that the total life span is hardly more than one year. Yet all attempts to breed the animal in captivity have utterly failed. Therefore, it is not possible to express the size of the embryo at the succeeding stages of development in terms of the time elapsed since fertilisation, as can be done with the usual laboratory animals.

Throughout this study the developmental stage of the embryo has been used as a substitute for the time since fertilisation. This proved to be a reliable indication; the fact that the twin embryos, one in each uterine horn, are always on exactly the same stage of development, indicates

already that this development proceeds with a clock-work precision. This was corroborated whenever two females with embryos in the same stage were available for study.

The segmentation of the egg ends in the 4-celled stage, when the early blastula is formed. At first the number of nuclei of the blastula can be accurately counted. So we have 8-celled, 16-celled blastulas, etc., but when there are more than forty nuclei it becomes increasingly more difficult to identify the separate nuclei in the sections and to count their number. The formation of the embryonic node starts when the blastula is composed of over 100 cells; the presence of this node characterises the blastocyst stage, and the size of the node can be used as a scale during this stage. A hollow next appears in the node, which is the primary amniotic cavity. The diameter of the so-formed amnio-embryonic vesicle then gives a reliable indication of the relative age of the embryo. Next follows the stage of the primitive streak. During this stage the age of the embryo can be gauged from its general form, although this cannot be expressed in numbers and therefore is a less exact indication of the age. Soon the first somites appear; they can be counted accurately in serial sections, and their number provides an infallible aid for expressing the age of the embryo in an accurate way. When 41 pairs of somites have been formed, the anterior ones start further differentiation and soon lose their identity. But by this time the embryo has grown large enough to measure its crown-rump length; mostly when one uterine horn with the embryo was sectioned, the contralateral one was used for measuring the length.

In a few instances exact cross-sections, starting in the mid-brain, were obtained of embryos in the somites stages, and then the length of the embryo could be measured in addition to counting the number of somites. For the sake of comparison it may be worth while giving this data. So it was found that an embryo with 14 somites was 2·6 mm. long, with 30 somites 3·05 mm., with 34 somites 4·5 mm., and an embryo with just over 41 somites, when the anterior ones become unrecognisable, was found to have a 4·9 mm. crown-rump length.

The crown-rump length of the foetus just before birth is about 40 mm.

In this way a scale could be established for the relative age of the embryo, and the changes taking place in the uterus could be dated with a fair amount of accuracy. The absolute age of the embryo at the succeeding stages, however, remains unknown.

As mentioned in a previous paper (van der Horst, 1946), during one season animals were collected regularly every week. After a period of anoestrus, lasting half a year, *Elephantulus myurus jamesoni* gradually comes into oestrus at the end of July or the beginning of August. Although there are individual variations, which may be considerable, this material

showed that the 10th of August, on an average, could be taken as the day when *Elephantulus* was in full oestrus and when fertilisation took place. The progress of the embryonic development in time could be followed from this material. It has to be added that about two days after parturition the female is fertilised again and becomes pregnant for a second time.

Of the six females collected on 7th October, three were in early pregnancy for the second time in the season, the other three had embryos of 18·5, 29 and 36 mm. length. On 14th October five animals were collected in early second pregnancy, and a sixth had an embryo of 28·6 mm. From this it follows that the gestation period is about eight weeks.

The material was too scanty and showed too great an irregularity to allow even an estimate of the absolute age of the embryo at any particular stage. But this material showed sufficient evidence to conclude that the development is exceedingly slow during the first part of pregnancy. At mid-term, *i.e.* after four weeks, the embryo is no longer than about 4 mm.; after another four weeks it has reached a length of 40 mm. After birth the measurements, of course, have to be taken in another way, yet they also give an indication of the growth. It appeared that in four to five weeks the young animal reaches the maximum size; during that time its length, without the tail, increases from about 5 to 10 cm.

The Systematic Position of *Elephantulus*.

The Macroscelididae, the family to which *Elephantulus* belongs, have been the object of research of many authors. Mostly the anatomy of the full-grown animal was studied. Only two publications by Gérard (1922, 1923) deal with the reproductive phenomena in *Nasilio*, one of the Macroscelididae. These papers only came to hand after the war, so they could not be considered in previous publications.*

The systematic position of the Macroscelididae and their relation to other mammals have given rise to great controversy. A short account of the literature on this problem has to be included here in order to give reasons for comparing the embryological development and placentation of *Elephantulus* with that of other particular groups of mammals, notably the Insectivores on the one hand and the Primates on the other.

Since Peters (1852) divided the mammalian order of the Insectivora into two groups—one, comprising *Galeopithecus*, *Tupaja*, and the Macroscelididae, characterised by the possession of a large caecum, whilst in the other, containing all the other Insectivora, the caecum is absent, to which groups

* Starck's publication (Starck, D., 1948. "Ein Beitrag zur Kenntnis der Placentation bei den Macroscelididen", Z. Anat. Entw. gesch., Bd. 114, p. 319) unfortunately came to hand only after this paper had gone to the press.

Haeckel gave the names of Menotyphla and Lipotyphla—the systematic position of the Macroscelididae has been a matter of great controversy up to the present day.

There is no doubt at all that the Insectivora, no matter whether they are divided into one or two or even three separate orders, are the most primitive of the monodelphic mammals, and amongst the Insectivores the Macroscelididae again occupy a very primitive position. It is, therefore, not surprising that Parker (1885) found great similarities between the skulls of the Macroscelididae and the Marsupialia. According to Broom (1902), the anatomy of the anterior nasal region of *Macroscelides* agrees closely with that of *Perameles*, and their relationship to the Marsupialia in this respect was confirmed by du Toit (1942). Elliot Smith (1902) laid emphasis on the remarkable combination of primate and metatheroid characters which the brain of *Macroscelides* presents. Gilbert (1944) showed that *Elephantulus*, in common with Monotremes, some Marsupials and a number of reptiles, normally has a paired post-renal vena cava. Also the fact that, although *Elephantulus* seems to have a uterus duplex, a differentiation between a uterus and a vagina has not been accomplished (van der Horst, 1942 *b*), may be regarded as very primitive, and the enormous number of eggs, 120 on the average, liberated at each ovulation points in the same direction (van der Horst and Gillman, 1941 *a*). In the latter respect, however, we see again that the Macroscelididae form a link between the reptilian ancestors and the higher mammals, as some species of the family Macroscelididae produce this large number of eggs, whereas others, like normal mammals, liberate only a few eggs (van der Horst, 1944 *b*).

It is, therefore, not surprising to find some features in the development of *Elephantulus* that can be regarded as very primitive, and that bridge a gap in this respect between the Marsupials and the Monodelphic mammals.

The Insectivora are generally regarded as the most primitive order of the Eutheria. Maybe just because of this they form a polymorphous group of animals, the members of which, or at least a number of them, are only loosely connected with each other (Weber, 1928). The Insectivores may show primitive characters which, just because they are primitive, may be found also in other orders of mammals, as well as characters of a more secondary, adaptive nature which show that they have diverged in different directions. For this reason a comparison of the placentation of *Elephantulus* with that of other Insectivores is very instructive, and it will be shown that in this respect there is, in this group of mammals, a greater divergency than in any other order, with the exception of the Primates.

The Menotyphla especially, to which the families Tupaiidae and Macroscelididae belong, have given rise to many disputes about their relationship. Gregory (1910) pointed out that the Menotyphla have many characters in

common with the Primates, and that, on the other hand, they show so many differences from the Lipotyphla that their retention in the order of the Insectivora is not warranted. Simpson (1931) in his classification of mammals expressed this relationship by removing the Primates from their usual position at the end of the row of Mammals to a place next to the Insectivora. As far as it concerns the Tupaiidae, the general opinion seems to be that they are nearly related to the Primates, or even that they have to be removed from the Insectivora altogether and placed in the order of Primates. According to Weber (1928), the arboricolous Tupaiidae correspond in many anatomical characters, especially with the also aboricolous Lemuroidea, and these characters can only partly be considered to be of an adaptive nature. Abel (Weber, 1928) is of the opinion that the Tupaiidae separated themselves from the rest of the Insectivora in the early days of their history and that they have developed along their own lines, which places them close to primitive Primates but not near the Lipotyphla. From his studies of the brain, the musculature and the skull, Le Gros Clark (1924, 1925) came to the conclusion that the Tree-shrews should logically be classified as primitive Primates and grouped with them, although they are much more primitive than any recent Primate and a considerable structural gap separates them. After her extensive comparison of different organ systems, it was apparent to Carlsson (1922) that the Tupaiidae cannot be classified with the Insectivores but that they form a suborder of their own amongst the Prosimiae.

On the whole, it seems that the Primate affinities of the Tupaiidae are well established. But regarding the Macroscelididae there is more difference of opinion. These two families are united to the suborder Menotyphla of the Insectivores by Weber, but he is not quite sure about the validity of the suborder. According to van Kampen (1905), the composition of the tympanic cavity is in agreement with the division of the Insectivores into Menotyphla and Lipotyphla, and this grouping appeared to Lyon (1913) to be a natural one. As mentioned above, Gregory (1910) keeps the two families together in the order Menotyphla, which with the Primates, etc. form the superorder Archonta, so the Macroscelididae are here far removed from the Insectivora. In a later publication (1921), however, he says: "This pre-primate stock is represented in the existing fauna by the Tree-shrews (family Tupaiidae), which are extremely primitive in many characters"; so one is left in doubt here whether the Macroscelididae also belong to the pre-primate stock or not.

In 1909, Albertina Carlsson was of the opinion that the Macroscelididae show affinities to two other Insectivore families, the Tupaiidae and the Erinaceidae, but in 1922 she came to the conclusion that the relation between the Tupaiidae and the Macroscelididae is a very remote one, the former are

removed from the Insectivores and form a suborder of their own of the Prosimiae, and the latter are nearly related to the Erinaceidae. Also Kaudern (1910) found a correspondence in the abdominal musculature between Tupaia and the Lemurinae, but not between Tupaia and the Nycticebinae, from which he concludes that Tupaia and the Prosimiae have a common but far removed ancestor. Lorenz (1927), who compared the hand of *Tupaia* with that of *Nycticebus*, finds them quite different, like Kaudern did the abdominal musculature, and so he concludes that *Tupaia* cannot be a primitive forerunner of the Primates.

Le Gros Clark (1932) points out that it is difficult to conceive two small mammalian brains which are more fundamentally different and divergent in their structure than those of *Macroscelides* and *Tupaia*, and he emphasises this by separating these forms into two distinct superfamilies, Macroscelidoidea and Tupaioidea. With this exception of putting *Macroscelides* and *Tupaia* into two superfamilies instead of families, he wishes to adopt the classification of Simpson, who, as said before, places the Tupaioidea amongst the Insectivora, yet in the same paper Le Gros Clark says that the Tree-shrews should logically be classified with the Primates and grouped with them. Also, in 1934, he wished to remove them from the Insectivora and to include them among the Primates. In an earlier paper (1928) Le Gros Clark came to the conclusion that the evidence of cerebral anatomy is quite compatible with Carlsson's hypothesis that the Macroscelididae branched off from ancient Erinaceidae.

From his studies of the tongue, Sonntag (1925) concludes that the Macroscelididae, Tupaiidae and Primates had a common origin from mesozoic Menotyphla, the animals which Gregory terms insectivorous pre-Primates. According to van der Klaauw (1929), the structure of the auditory bulla shows that the Macroscelididae are more nearly related to the Lipotyphla than the Tupaiidae, but also the latter are more insectivorous-like than primate-like. Again a different opinion is held by Frechkop (1931). By comparing the teeth in particular, and also the skull, he came to the conclusion that the Tupaiidae have some affinities with the Primates, but that the Macroscelididae are widely different from them and are on the way that leads to the Ungulates.

More recently, Evans (1942) came to the conclusion that comparative osteological studies show that the Macroscelididae are much more closely related to the Tupaiidae than to the Erinaceidae, and that these two families should not be separated. The Macroscelididae are shown to have almost all of the lemuroid features found in *Tupaia*, and, on the basis of their lemuroid osteological characters, the Macroscelididae show about as much justification for placing them with the lemurs as does *Tupaia*, and if the latter is placed with the Lemuroidea the former should be also.

Roux (1947) concluded that the development of the skull supplies ample justification for regarding the Menotyphla as a separate order, distinct from, but allied most closely to, the Insectivores.

From this summary of the literature one can conclude that the Macroscelididae are very primitive mammals, and therefore a comparison with the Marsupialia is warranted. They may be related to other Insectivora, more particularly to *Erinaceus*, which is considered to be very primitive amongst the Insectivora, and, as will be shown, there are reasons for accepting this relationship. On the other hand, their affinities with the Primates are often denied, and if they are accepted, it is because of the relationship between the Macroscelididae and the Tupaiidae. A comparison of the placentation of *Elephantulus* with that of the Primates is therefore of great interest. It will be shown that from this point of view there is more reason to link up *Elephantulus* with the Primates, and with the Anthropoidea in particular, than there is to connect Tupaiia with the Lemuroidea.*

Descriptive Part.

In the following pages different sections will be devoted to the history of the placenta, the uterine glands, etc. during pregnancy. These organs are, of course, closely connected with each other in their metamorphoses. Yet an effort has been made to give as complete a picture of the changes taking place in each of them as possible. Therefore a certain amount of repetition could not be avoided.

The External Form of the Uterus during Pregnancy.

During pregnancy the uterus of *Elephantulus*, in particular the conceptus, undergoes some transformations in its external form, which are characteristic for the succeeding stages of gravidity.

Before proceeding to an analysis of these transformations, it is desirable to outline briefly the main features in the morphology of the non-pregnant uterus. A more detailed account of the structure of the entire reproductive tract has been given elsewhere (van der Horst, 1942 *b*). In general, the genital tract consists of a median uterus and two horns, the latter being approximately 1·5 cm. in length. In the non-pregnant, parous animal, in early pro-oestrus, after the period of anoestrus (fig. 1, *a*) each uterine horn can be divided into two parts, viz. a caudal and thicker portion, and a cranial part which is abruptly continuous with the narrow Fallopian tube; the latter in turn expands at the ampullary end to enclose the ovary. The

* See also Horst, C. J. van der, 1949. "The Placentation of *Tupaia javanica*", Proc. Akad. Wet. Amst., vol. 52.

median uterus has approximately the same diameter as the lower part of the horn. The mesometrium is attached laterally and slightly dorsally to each uterine horn. This permits the orientation of the uterus in terms of mesometrial and anti-mesometrial poles.

At the time of ovulation (fig. 1, *b*), the caudal half of each uterine horn swells in such a way that the oval shape, as seen in cross-section during anoestrus (fig. 2), is converted into a round one characteristic of oestrus (fig. 3). This swelling tapers gently in a cranial direction, but ends more abruptly where it joins the median uterus. The diffuse character of the swelling during oestrus provides, neither microscopically nor macroscopically, any indication that all the events enacted in the endometrium during the menstrual cycle and during pregnancy will be strictly confined to a very circumscribed part of the uterus. And in a section of the uterus at the height of oestrus (fig. 3) there is nothing in the structure of the endometrium whereby the mesometrial pole distinguishes itself from the rest of the uterus, notwithstanding the fact that implantation takes place here.

A single embryo implants at a restricted site in the caudal part of each uterine horn. Consequently all modifications in shape during pregnancy are confined to this part (fig. 1), while the cranial portion of each horn and the median uterus scarcely evince any change. The median uterus remains practically unaltered even when the embryo is nearing the end of gestation (fig. 1, *n*).

From the time of implantation until the end of pregnancy the uterus sequentially assumes three distinctive shapes: a hemispherical, a spherical, and a cylindrical.

Immediately after the embryo reaches the implantation site, the structural changes induced in the decidua lead to a local excentric enlargement of the uterus, confined to the mesometrial pole. At the blastocyst stage and before implantation, a noticeable swelling is at once apparent (fig. 1, *c*). This swelling is confined to a small part of the uterus. At first it has a more conical shape, and then gradually acquires its hemispherical form (fig. 1, *d*, *e*), which is well developed when the embryo has thirteen somites (fig. 1, *f*). At this stage in cross-sections it is not easily possible to appreciate the hemispherical shape of the uterine swelling (figs. 9, 14). By contrast a longitudinal section at once reveals the remarkable excentric, but localised growth which has produced the characteristic shape of the conceptus (fig. 13). Although the swelling increases in size, its hemispherical form is maintained until the embryo has developed over 40 somites. In cross-section, at this stage, a slight bulging towards the anti-mesometrial pole may be evident (fig. 18), but this is only observed externally when the embryo is 6 to 7 mm. long (fig. 1, *h*).

With the remoulding of the interior of the uterus, which results in the

destruction of the bursa embryonica (figs. 17, 18, 19) (see p. 478), the uterine swelling gradually changes its shape from a hemisphere to a sphere (fig. 1, *h*, *i*, *j*, *k*). The spherical form is already well stabilised when the embryo is 7·4 mm. in length, and persists until the embryo is about 20 mm. long. Throughout this period there is, of course, a steady increase in the size of the swelling, *i.e.* from a diameter of 9·5 mm. to one of 22 mm. This change from a hemisphere to a sphere is largely due to an extension of the anti-mesometrial side of the uterus, with the result that the embryo gradually assumes a position in the centre of the uterus.

The uterine swelling acquires a more cylindrical shape when the embryo has reached a length of over 20 mm. Whereas the mediolateral axis has already achieved its maximum length when the embryo is 19 mm. long, and the uterus still has its spherical shape, henceforth the enlargement of the uterus occurs in a cranio-caudal direction. At first the swelling is elliptical (24·5 mm. embryo, fig. 1, *l*), and this is maintained during the period that the embryo increases by another 10 mm. (fig. 1, *m*). The broadening then occurs at the cranial and caudal poles, until eventually the swelling is more cylindrical (fig. 1, *n*). This change, from the spherical to the cylindrical shape, is associated with a twofold increase in the cranio-caudal axis of the conceptus. It should be mentioned, too, that the dorso-ventral axis of the uterine swelling is much greater than the mediolateral one.

The part of the uterus in front of the swelling, as well as the median uterus, undergo no change in girth throughout gestation. Even when the conceptus increases in length (fig. 1, *n*), the cranial part of the uterine horn maintains the same length as before pregnancy (fig. 1, *a*, *n*). This unquestionably indicates that the growth of the conceptus is confined to a very circumscribed part of the uterus.

Throughout the early part of gestation there is a direct communication between the cranial part of each horn and the median uterus, despite the interposition of the large uterine swelling. This is attained by the preservation of a part of the uterine lumen as a continuous canal in the anti-mesometrial pole (fig. 15). Since in early pregnancy the conceptus develops excentrically, this communication is located at the base of the swelling and along the medial side of each horn. When the conceptus assumes a spherical form, the communication between the two unaffected parts of the uterus is interrupted by the enlarging embryo.

As has been mentioned, the mesometrium is attached to the lateral side of the uterine horn, but slightly off the centre in a dorsal direction (fig. 2). The embryo implants itself at the mesometrial pole of the endometrium, corresponding to the exact midline of the uterus. This means that the embryo occupies a position slightly ventral to the line of attachment of the

mesometrium. Consequently, when the conceptus enlarges, the mesometrial attachment simultaneously acquires a more dorsal position, which in cross-section appears to be lateral (fig. 7). Despite the great enlargement of the decidua, the original midline of the uterus remains fixed. In support of this statement it might be added, that when the mesometrium is situated well laterally, the axis of the placenta still passes through the original anti-mesometrial pole of the uterine horn (fig. 18). When the hemispherical shape of the conceptus is fully established, the line of attachment of the mesometrium is completely lateral. If the line of attachment of the mesometrium had continued to be the fixed anatomical reference point, then the implantation site would have shifted to a lateral position. However, since the implantation site is fixed and originally corresponded to the mesometrial pole of the uterus, despite the change in position of the mesometrial attachment, the implantation site will be regarded throughout this study as being mesometrial. Indeed, this lateral attachment of the mesometrium is only temporary. With the change of the conceptus, from a hemispherical to spherical form, the line of attachment of the mesometrium seems to shift back to its original position near the axis of the placenta (figs. 20, 21).

Only a restricted part of the uterus is immediately involved in the changes occurring during pregnancy. The swelling is, and remains, confined to the caudal part of each uterine horn, and the originally much longer cranial part apparently remains totally unaffected. On the other hand, the striking changes that occur in the shape of the conceptus can be correlated with the size of the embryo at successive stages of pregnancy.

Placentation.

The whole process of placentation can be subdivided into a number of successive stages, viz. the stage of pre-implantation, the stage of penetration, the stage of formation of the ectoplacenta, and finally the stage of formation of the definitive placenta.

Pre-implantation Phenomena.—Attention has already been drawn to the reactions taking place in the embryo and the uterus before actual implantation occurs (van der Horst and Gillman, 1942 *a*). The embryo arrives at the implantation site in the 4-celled stage (figs. 4, 22). By this time the uterus has lost its oedematous condition, characteristic of the period of ovulation. The stroma is now dense, the glands are reduced in size, and the epithelium lining the uterine cavity has a uniform thickness throughout, except for some irregular folds at the anti-mesometrial pole. The sequence of events, enacted in the uterus soon after the arrival of the embryo at the presumptive implantation site, is depicted in figs. 5–9 and 22–28. The embryo enlarges by rapid multiplication of the cells and a

corresponding increase in size of the blastocoel (figs. 25, 26) (van der Horst, 1942 *a*). Coincident with these changes in the embryo, the uterus exhibits noteworthy reactions confined to the endometrium near the mesometrial pole; there the embryo-chamber forms, the stroma becomes oedematous again, the glands dilate their upper third, the chamber epithelium becomes eosinophilic and shows signs of early thickening and vacuolation (fig. 28).

Notwithstanding these remarkable modifications in the endometrium, the embryo itself, although considerably enlarged, does not exhibit any outward sign of being polarised. All the cells lining the blastocoel have the same appearance and participate equally in the formation of the embryo proper. Structurally these cells afford no indication of their destiny, nor is it possible to predict where the chorionic villi will first develop (fig. 24). Morphologically, therefore, the embryo does not show any indication of polarity. Thereafter, the embryo rapidly develops into a blastocyst in the manner previously described (van der Horst, 1942 *a*), and at the same time the uterus continues the series of transformations preparatory to nidation (van der Horst and Gillman, 1942 *a*).

Before nidation occurs, however, the embryo passes through a number of developmental stages (figs. 27, 28). After reaching the blastocyst stage, the ectodermal cells become aggregated into a solid spherical mass, while the entoderm is represented by irregularly shaped cells scattered inside the trophoblast; some of these entodermal cells are already in the process of spreading over the embryonic node (fig. 29).

By this time the trophoblast shows a definite polarity, and a placental and an obplacental area can be recognised. In the latter, the trophoblast consists of a thin layer of cells, indistinguishable from those lining the entire outer surface of the embryo at the earlier stage. In the placental part, however, two main reactions are evident: the first is a thickening of the trophoblast, which here consists of two to three layers, the individual cells being larger than those in the obplacental area of the trophoblast; the second reaction manifests itself in the appearance of a small number of fine finger-like outgrowths of cytoplasm containing small clusters of nuclei (fig. 31). These cytoplasmic outgrowths extend in the direction of the chamber epithelium. Initially they resemble large pseudopodia, into which later the clusters of nuclei migrate. The absence of cell walls, and the crowding of nuclei into the cytoplasm of such an excrescence, indicate the emergence of the plasmoditrophoblast.

Along the annular demarcation line, between the placental and obplacental area of the trophoblast, three or four of these finger-like processes are arranged. Corresponding to this demarcation line, between the placental and the obplacental part of the trophoblast, an annular line in the uterine epithelium is now apparent (fig. 31). At the placental side of this line the

uterine epithelium, lining the embryonic chamber, has undergone a coagulative necrosis, whereas the epithelium, related to the obplacental pole of the embryo, remains unaffected except for the presence of small papillary projections. It is remarkable that the same sharp delimitation into two areas, exhibited by the trophoblast, is also reflected in the surface epithelium of the uterus.

The finger-like processes, growing out from the trophoblast in the annular demarcation line, establish contact with the uterine epithelium just where the necrotic lining of the chamber becomes continuous with the seemingly unaffected uterine epithelium. Thus on the one side of these trophoblastic outgrowths there is massive necrosis of this epithelium, whereas on the other side it remains perfectly healthy. Whatever the mechanism for this sharp demarcation may be, it is evident that the stimuli emanating from the trophoblast are able to operate over a very circumscribed area only. It will be recalled that, at a slightly earlier stage in the development, the chamber epithelium was greatly thickened due to the accumulation of cells, as well as to the increase of fluid in the form of large vacuoles (fig. 28). However, as soon as the finger-like processes differentiate and extend in the direction of the epithelium, the fluid disappears, the outline of the individual cells in the chamber epithelium is lost and the nuclei become hyperchromatic. With this dehydration of the chamber epithelium the nuclear and cytoplasmic debris coagulates into a relatively dense mass (fig. 32).

Besides the finger-like processes in the zone of demarcation between the two parts of the trophoblast, there are, in addition, a few more similar processes found towards the placental pole of the embryo. Such processes, however, are not always slender, for short robust processes may be seen which, like the slender variety, make only light contact with the coagulated chamber epithelium.

The reactions of the decidua are portrayed in figs. 4–9. Briefly, they consist of a compression of the dilated uterine glands, and an intensification of the decidual reaction which is related to the region of the chamber only.

By the time the complete penetration of the chamber epithelium has been achieved, the embryo has progressed so far that a primary amniotic cavity has now been differentiated (fig. 31). The amnio-embryonic vesicle, however, has not yet arrived at the future placental pole of the embryo. The entoderm has proliferated to such an extent that it forms an uninterrupted lining both to the embryonic node as well as to the trophoblast. The placental cone of the trophoblast now stands in sharp contrast to the part of the trophoblast related to the yolk-sac. This obplacental part of the embryo has greatly enlarged to form a distended vesicle, projecting well into the main uterine cavity. Covering this vesicle is a much thinned

trophoblast, now lined completely by entoderm. By contrast, the placental cone of the trophoblast is from two to four times as thick as the obplacental part.

The great mitotic activity seen in the placental trophoblast fulfils a dual role: firstly, it continually adds cells to the cytotrophoblast; secondly, it provides the nuclei that migrate into the enlarging processes of the plasmoditrophoblast. It may be stated with reasonable assurance that mitosis is confined strictly to the cytotrophoblast, and never occurs in the plasmoditrophoblast. Neither has *a*-mitosis been observed in the plasmoditrophoblast.

The outstanding feature is the technique adopted by the plasmoditrophoblast for the penetration of the coagulated remnants of the chamber epithelium. Soon after contact is established between the cytoplasmic outgrowth of the trophoblast and the chamber epithelium, the process of penetration is achieved by a lengthening of this finger-like outgrowth of cytoplasm, associated either with a local digestion of the coagulum, or it may pass in between the remnants of the degenerated cells of the chamber epithelium. Once this cytoplasmic outgrowth has passed through the whole thickness of the chamber epithelium and has reached the basement membrane, it spreads out at right angles to the direction of penetration (fig. 32).

Coincident with the appearance of these outgrowths, nuclei concentrate in the trophoblast at the attached base of the outgrowth. While a few of these nuclei pass down into the process, as it penetrates the epithelium, as soon as the outgrowth broadens out against the basement membrane, a rapid migration of nuclei occurs leading to the result shown in fig. 32. Here it is evident that the multinucleated plasmodial outgrowth, lying in contact with the basement membrane, is connected by a narrow stalk to the thickened cytotrophoblast. The orientation of the nuclei in the stalk, as well as in the club-shaped part of the plasmoditrophoblast, reveals that the nuclei are actually passing down the stalk. These nuclei are arranged in the same way as are the red blood corpuscles in a capillary. Once they have reached the club-shaped end the nuclei form a dense mass, from which they are diverted into the rest of the cytoplasm.

The mechanical effect of these outgrowths of the plasmoditrophoblast is such that it anchors the young embryo temporarily to the chamber epithelium. This anchorage is brought about by a broad disc of plasmoditrophoblast spreading out along the basement membrane, whereas only a thin stalk passes through the coagulated chamber epithelium. Such anchorage as exists could not be effective unless, as has been suggested, the necrotic chamber epithelium was dehydrated sufficiently to increase the consistency of the cellular debris.

Several of these short anchoring villi appear either simultaneously or in

rapid succession. As the club-shaped ends spread out along the basement membrane they establish contact with each other, and may fuse to form an irregular network lying immediately adjacent to the basement membrane. This network is then connected to the cytotrophoblast by a series of delicate stalks. These stalks will later become the loci from which the digestion of the chamber epithelium is completely effected.

At the attachment of the stalks to the placental cap of cytotrophoblast, active proliferation of cells is evident. At the same time these stalks thicken and become shorter. Whether this reaction is due to a differentiation of the plasmoditrophoblast into a cellular cytotrophoblast, or whether the cytotrophoblast actually extends along and replaces the stalks, is difficult to decide. Whichever the case may be, the embryo eventually establishes an intimate contact with the remnants of the coagulated chamber epithelium. By the substitution of the cytotrophoblast for the digested epithelium, the embryo progressively occupies and plugs the wound created in the uterine epithelium.

At the close of this first phase of penetration, the embryo has developed a large amnio-embryonic vesicle, situated near the placental cap; the yolk-sac, now completely bilaminar, is greatly distended; the placental cap, consisting of several layers of cells, is pressed against the remnants of the chamber epithelium; and the embryo is anchored by short, broad stalks attached to the plasmoditrophoblast, which lies against the still intact basement membrane of the chamber.

The Penetration.—The next stage is characterised by the destruction of the basement membrane, through which the plasmoditrophoblast passes into the decidua, to form suddenly long anchoring villi. The behaviour of the plasmoditrophoblast, however, depends largely upon the extent of the dilatation of the subchamber blood-vessels. If such a blood-vessel is locally very distended, then the plasmoditrophoblast, coming in contact with it immediately after erosion of the basement membrane, starts to envelop that blood-vessel with a network of multinucleated, pseudopodium-like outgrowths. Such a stage is depicted in figs. 33 and 34. On the other hand, if the blood-vessels are not excessively distended, then, immediately after disruption of the basement membrane, the plasmoditrophoblast penetrates to a great depth into the decidua.

In fig. 33 the basement membrane is already disrupted. The sub-epithelial blood-vessel, in this particular instance, is rather distended, with the result that a local concentration of the plasmoditrophoblast represents the first stage in the envelopment of the blood-vessel. A second phase in this process is shown in fig. 34, where the outstanding feature is the envelopment of the blood-vessel by the thickened plasmoditrophoblast on the one side and by the cytotrophoblast on the other. It is evident from this figure

that the embryo is not potentially endangered by the premature opening up of this large vascular channel. As a compensating measure, the embryo is tightly drawn against the decidua and in this way plugs the wound. Once the blood-vessels are well surrounded, the plasmoditrophoblast then proceeds deeply to invade the underlying decidua.

While the precocious dilation and erosion of a subchamber blood-vessel may temporarily retard the plasmoditrophoblast in its further invasion of the decidua, such a delay is only of short duration. Once the encirclement of the blood-vessel has been achieved, deep penetration occurs in the same way as in those instances where the blood channel is represented by a rather small capillary. The only difference at later stages is expressed by the presence of a larger mass of plasmoditrophoblast near the embryo.

Having pierced the basement membrane, the plasmoditrophoblast deeply penetrates into the substance of the decidua to form long root-like outgrowths. From the two reconstructions (figs. 39, 40) it appears that there are only a few of these long roots. These outgrowths usually spread along the elongated necks of those glands opening into or near the chamber. The plasmoditrophoblast, as it were, shears off the gland epithelium from the underlying decidual tissue, producing only local injury to the epithelium of the gland without any gross effect on the related decidua, except near the opening of the gland into the uterine cavity (figs. 35, 42). When a part of the gland is completely isolated from the decidua by a mass of plasmoditrophoblast its epithelium degenerates, due to interference with its nutrition. While the main root tends to follow the glands, the branching terminals are apparently attracted by the blood-vessels which they closely encircle (fig. 43). In the depth of the decidua, however, despite the burrowing activity of the plasmoditrophoblast, there is scarcely any evidence of destruction either of the decidua or of the glandular epithelium. Even where the branching roots establish intimate contact with the dilated blood-vessels, the intima remains intact. The peculiar manner in which the plasmoditrophoblast envelops the dilated blood-vessels in the decidua shows that the erosion of the endothelium is certainly not affected by the plasmoditrophoblast, but indeed is achieved by direct contact of the cytotrophoblast.

The stage of the maximum development of the deep anchoring roots is portrayed in figs. 39–41. Fig. 39 is a picture of a wax reconstruction of a whole embryo, and shows, in a way, all the end branches of the deep roots which arborise around the glands and the blood-vessels. Fig. 40 portrays a single section of the embryonic vesicle with its cytotrophoblast, to which is attached a graphical reconstruction of the plasmoditrophoblast; and fig. 41 provides part of a section through the uterus with the embryo *in situ*. From these figures the length of the roots, as well as the complexity of the

terminal arborisations, can be readily appreciated. Despite the robust character of the plasmoditrophoblast, the attachment of the latter to the cytotrophoblast is extremely delicate (fig. 42). The majority of the primary villi are not associated at all with the plasmoditrophoblast.

When these long roots have been established, short primary villi, consisting of cytotrophoblastic cells, grow into the decidua. In so doing, the related decidual cells are progressively destroyed, the cytoplasm being first affected. The nuclei are more resistant and degenerate later. This is further evidence that the digestion of the maternal tissues is accomplished solely under the influence of the cytotrophoblast. Penetration of the embryo into the superficial layers of the endometrium is facilitated by the plasmoditrophoblast and then consolidated by the cytotrophoblast.

The Formation of the Ectoplacenta.—The next significant step in the formation of the placenta is characterised by (1) the formation of numerous thin chorionic villi, (2) the establishment of the intervillous circulation, (3) the atrophy of the deep anchoring roots of the plasmoditrophoblast, and (4) the termination, or at least a marked slowing down, of the invasion into the decidua of the cytotrophoblast.

The primary villi invade the superficial layer of the decidua in the form of broad cords of cells attached to the placental cap of the trophoblast. The latter consists of several layers of cells forming a compact mass interposed between the villi and the amnio-embryonic vesicle (fig. 40). When a few layers of decidual cells have been destroyed, with consequent opening of the blood-vessels, the broad chorionic villi, as well as the thick placental cap, become transformed into an irregular delicate meshwork of fine cellular strands (fig. 35). This meshwork is elaborated by a rearrangement of the constituent cells into trabeculae, which are separated by narrow clefts. As soon as the blood of the opened capillaries penetrates between these trabeculae, the intervillous circulation is inaugurated. This canalisation of the placental cap not only lengthens the villi, but is also responsible for their more slender appearance. The cross-connections established between these slender villi by means of thin, stretched cells convert the intervillous space into an open meshwork, through which the maternal blood circulates (fig. 36).

It will be recalled that the vascularity of the uterus is not well marked prior to the erosion of the chamber wall. Thereafter the vascular bed comes into great prominence (fig. 10). This is caused by a remarkable dilatation of the coiled arterioles in the decidua, and also by a widening of the corresponding veins. These enlarged, thin-walled arteries narrow considerably as they approach the chamber, where they terminate in a network of distended capillaries (fig. 30). In fact, these capillaries sometimes become so large that they may temporarily modify the normal sequence

of penetration by the long anchoring villi (fig. 34). A significant increase in the vascularity occurs when the chorionic villi pierce the basement membrane to penetrate into the decidua (fig. 33). Dilated arterioles are now seen in a section at two levels in the uterus. The first is situated in the deeper part of the decidua compacta. These vessels, as we have seen, are the first to become evident; they are much more extensive than the vessels at the second level, which become manifest a little while before the chamber epithelium is destroyed. The latter vascularity is confined to the region immediately contiguous with the penetrating villi. It is noteworthy that the diameter of the intervillous space is greater than the dilated arterial segment feeding these spaces. This implies that the blood-flow is sluggish through the intervillous space.

Once the trophoblastic villi have entered the decidua, the decidual cells near the villi collapse; their cytoplasm contains numerous granular bodies, while in the nuclei the chromatin is aggregated into irregular clumps or spherules clustered tightly together. The reticulum related to these cells becomes, at the same time, obviously accentuated. It is apparent that the decidual cells undergo degeneration by coagulation rather than by liquefaction. The related reticulum is unquestionably more resistant, so that the chorionic villi are embedded in this reticulum supporting the two or three layers of degenerated decidual cells, which intervene between the invading chorionic villi and the seemingly unaffected decidua. A fibro-cellular layer is thus created parallel to the placental cap and at right angles to the chorionic villi (figs. 35, 36). It consists of an interlacing network of prominent fibres, between which are found the compressed remains of dead and dying decidual cells.

Soon after the development of the fibro-cellular layer, however, the vitality of the long anchoring villi significantly deteriorates. The fibro-cellular layer develops in relation to the delicate attachment of the deeply penetrating roots of the plasmoditrophoblast to the short villi of the cytotrophoblast.

The earliest manifestation of this decreased vitality of the plasmoditrophoblast expresses itself in a loss of the translucent appearance of the cytoplasm, an increase in the fibrillae, and a hyperchromasy of the nuclei which are now chiefly concentrated in the centre of the strand (fig. 43). Shrinkage of the cytoplasm leads to a reduction in the diameter of the root and in section a root may easily be mistaken for a giant decidual cell. In this fashion the plasmoditrophoblast is slowly absorbed until it ultimately disappears. The destruction of these long anchoring villi of the plasmoditrophoblast occurs simultaneously with the emergence of a new mechanism for fixing the embryo in the uterus. This mechanism is represented by the lenthening cytotrophoblastic villi becoming

enmeshed by the thickened fibres related to the coagulated decidual layer (fig. 36).

In this way the thickened reticulum of the decidua acts as a supporting meshwork to the invading outgrowths of the trophoblast. This early attachment of the chorionic villi by means of reticular fibres implies that the roof of the intervillous space now consists of a swollen reticulum, collapsed and coagulated small decidual cells and some large giant cells. The space between the villi is mainly filled with maternal blood. Although the giant cells are found chiefly in the roof of the intervillous space, these decidual cells may frequently be encountered within the intervillous spaces themselves, particularly in the young placenta.

It is evident that the small decidual cells are more susceptible to the cytolytic action of the trophoblast than the giant cells. Whereas the small decidual cells become liquefied and their position is indicated by the swollen surrounding reticulum only, the giant cells shrink but retain their shape for a considerable time, such as is characteristic of the events in coagulative necrosis.

At first the intervillous spaces are filled with dying and dead cells (fig. 35). But when the process of penetration slows down, the destruction of more decidual cells does not occur so rapidly, and the necrotic debris is slowly digested (fig. 37). This removal of the debris materially widens the intervillous spaces.

At the periphery of the placenta the surface epithelium is also destroyed, and the chorionic tissue is supported by a thickened reticulum derived from the decidua. In this way the placenta is sealed off from the uterine cavity. A stage in this process can be seen in fig. 36.

The penetration of the basement membrane of the embryo-chamber, the formation of the long root-like outgrowths of the plasmoditrophoblast, and their subsequent degeneration, together with the formation of the primitive cytotrophoblastic villi, which are enmeshed in a reticulum containing necrotic decidual cells, characterise the processes involved in the provisional fixation of the young placenta to the uterus. Henceforth the growth of the placenta occurs mainly in the direction of the uterine cavity, while further penetration into the decidua is sharply reduced.

From the late amnio-embryonic vesicle stage, during the emergence and disappearance of the primitive streak, which is succeeded by the formation of the central nervous system, until the embryo is in the 12- to 14-somites stage, no fundamental departure occurs in the placental organisation from that shown in fig. 36. Throughout this whole period in the embryonic development emphasis is placed on growth, and to a lesser extent on differentiation. The broad features of the structure of the placenta, as shown in fig. 36, consist of a cellular placental cap to which the embryo is loosely

attached. Numerous strands of trophoblastic cells, forming the delicate villi, radiate from this cap, and are attached to the decidua by a reticular meshwork derived from the maternal tissues. Wide blood-filled sinusoids envelop these chorionic villi. Further erosion of the maternal tissues, and corresponding penetration by the embryo, has been brought virtually to a standstill, with a consequent demarcation of the foetal from the maternal tissue.

Once the foetal and maternal junction has been relatively stabilised, the placenta increases in thickness by growth in the direction of the uterine cavity. In the early primitive streak stage about two-thirds of the placenta extends into the uterine cavity, and the remaining one-third is embedded in the decidua (fig. 37). This discrepancy becomes more pronounced when the placenta is fully formed.

From fig. 37 it is evident that the placenta can be divided into two regions on the basis of structure, namely, an anchoring and a spongy part.

The anchoring part consists of irregular strands of chorionic cells enmeshed in a lacework of reticular fibres derived from the decidua. In this part of the placenta, the chorionic cells with their thick membranes, clear cytoplasm, centrally placed nucleus, suspended by delicate cytoplasmic strands, are reminiscent of plant-cells. The discrete character of these anastomosing strands of cells is further emphasised by the surrounding reticular fibres. While the decidual cells in immediate contact with the cytotrophoblast are for the most part destroyed, nevertheless a few survive and may be seen lying scattered between the chorionic villi. As a rule these cells are small and atrophic, with a shrunken nucleus and greatly vacuolated cytoplasm; occasionally a small giant cell can also be identified. In this latter instance the cytoplasm is eosinophilic and finely vacuolated, the nucleus is vesicular with two to four masses of heterochromatin.

On the periphery of the placenta the anchoring part is sharply demarcated from the underlying decidua by a distinct layer, consisting largely of hyaline material in which a few nuclei are embedded. The adjacent decidual cells are showing evidence of atrophy, and the granular intercellular substance is continuous with the eosinophilic hyaline layer. Towards the centre this hyaline layer becomes discontinuous, and consequently it is not so easily recognised. Beyond the attachment of the placenta an irregular cone of giant decidual cells forms a notable feature.

The spongy layer forms the thicker part of the ectoplacenta. It consists of numerous trabeculae forming a complex sponge-like network. These trabeculae are especially tortuous towards the centre, and are straighter at the periphery of the placenta. The intertrabecular space is occupied by lacunae, which may be wide in one part and of capillary dimension in

another. The trabeculae may be one or several cells thick. These cells are characterised by the thick cell membrane bordering the sinus, and in haematoxylin and eosin preparations, by relatively clear cytoplasm with eosinophilic granules; the large nucleus may assume many bizarre shapes, so that often a single section may give the impression that these cells are binucleated. The nuclear membrane is very distinct, and it encloses a clear nuclear sap with scanty chromatin and two nucleoli encircled by heterochromatin.

The radiating arteries, at the embryonic side of the placenta, are completely embedded in the substance of the spongy part. The surface of the placenta, bordering on the embryo, is thus formed by a continuous layer of cells. Immediately deep to the radiating arteries, small clusters of actively proliferating nuclei can be found, but no cell membranes can be discerned in these clusters. These nuclei are responsible for the further growth of the placenta.

An intraplacental circulation is now well established. As a rule two arteries pass, by a direct course, through the whole thickness of the placenta, and divide into a number of radiating branches. The latter are separated from the extra-embryonic coelom by only a single layer of trophoblastic cells, forming the outer layer of the placenta. The radiating vessels communicate with the complex lacunar system, which in turn is drained by several small uterine veins. These veins, at irregular intervals, perforate the anchoring network and the hyaline layer on their way via the decidua to the main uterine vein. The circulation through the placenta is noteworthy in so far as the direction of the flow in the lacunar system is away from the embryo and towards the decidua.

At the 13-somites stage, shortly before the allantois establishes contact with the placenta, the characteristic features of the placenta are as follows (fig. 15):—

(1) A twofold increase in the thickness of the placenta, as compared with that at the primitive streak stage, can be observed. This increase in thickness is due mainly to an enlargement of the spongy layer.

(2) The anchoring part of the placenta reveals a renewed activity of the chorionic cells. At an earlier stage (fig. 37) the junction between the placenta and the decidua was represented by a meshwork of fibres in which the plant-like chorionic cells were embedded, producing in this way a firm union between the foetal and maternal tissues. At the 13-somites stage, however, there is unmistakable evidence of a renewed vigour of these chorionic cells. Mitotic figures can be seen between the spongy and anchoring parts of the placenta. This proliferation leads to the formation of multinucleated strands of chorionic tissue. The strands radiate through the reticulum to penetrate into the decidua. As will be shown later, this

penetration culminates in the complete destruction of the decidua and the final stabilisation of the placenta.

(3) Apart from its increased thickness, the noteworthy feature of the spongy layer is the accumulation of round, discrete, intensely eosinophilic globules throughout the cytoplasm of the cells. In van Gieson preparations, this layer can easily be identified under low power of the microscope as a red staining zone wedged in between the anchoring part and the proliferating layer related to the radiating vessels. These eosinophilic granules, similar in many respects to those which will be described later as occurring in the decidual cells, first make their appearance in this part of the placenta when the embryo is in the primitive streak stage.

(4) Lying in the lacunae, more especially at the junction of the spongy and anchoring parts, are emboli of giant cells of decidual origin. These giant cells enter the decidual artery and are transported through the placental artery to the wider sinus, to be trapped in the narrow pre-venous sinus near the anchoring zone. Occasionally, such a giant cell may be found in the large sinus immediately underneath the embryo. These emboli provide confirmatory evidence of the direction of the circulation through the placenta.

(5) Evidence for the continued growth of the placenta is to be found in the irregular nests of nuclei situated deep to the radiating vessels. Here as many as a dozen mitotic figures may be seen in a single high-power field.

(6) The radiating vessels slightly protrude above the inner surface of the placenta, with the chorionic mesoderm insinuating itself into the crevices between the vessels. The walls of these vessels, derived from the trophoblast, are different from the tissue in the rest of the ectoplacenta, in so far as the nuclei are larger and the cell membranes cannot be discerned.

(7) The chorionic mesoderm forms a single, and mostly regular, layer of cells lining the embryonic surface of the placenta, and does not penetrate into the ectoplacenta. Here some mitotic activity can be observed.

As far as the placenta itself is concerned, no gross modification in structure occurs between the 12- and 18-somites stages. However, the 18-somites stage becomes a significant milestone in placental development, because, for the first time, intimate contact is established between the embryo and the placenta by the allantois. Hitherto the only existing connection between embryo and placenta was provided by the *a*-vascular chorion laeve, which at the most was only an indirect one, via the yolk-sac (fig. 44). This shows that, throughout this early period of development, the embryo was not immediately dependent for its nutrition on the placenta. The large, and richly vascularised, yolk-sac facilitated the transference of almost all the nutriment elaborated and secreted by the uterine glands.

The Formation of the Definitive Placenta.—The precise moment when

the allantois first establishes contact with the placenta could not be ascertained. This contact certainly does not exist in any of the several 13- or 14-somites stages available for examination. All endeavours to obtain embryos with 15, 16 or 17 somites have failed, whereas an uninterrupted series of developmental stages from the 18-somites stage onwards could be examined. In the 18-somites stage the allantois has made contact with the placenta.

The contact of the allantois with the placenta is at first restricted to a very small area; at the stage shown in fig. 45 this area extends over 0·3 mm.^{2} only. The allantois brings with it abundant mesenchym and foetal blood-vessels, whereas the allantoic cavity, at this stage, is rather restricted. The part of the allantois near the placenta constitutes a region of active growth, as evidenced by the large number of mitotic figures present in the sections. The mesoderm of the allantois, where it touches the placenta, becomes indistinguishable from the chorionic mesoderm that was there before, and, closely pressed against the surface of the placenta, it insinuates itself between the arcades formed by the protruding radial vessels of the placenta.

In the 18-somites stage the allantois still has the form of a curved cylinder (fig. 45). At once further growth of the allantois is directed towards the covering of the whole inner surface of the ectoplacenta. This is already initiated in the 19-somites stage, and in the 21-somites stage the allantois has covered more than half of the surface of the placenta (fig. 38). By the time the embryo has 27 somites, the placenta is completely covered by the allantois (fig. 17). The allantois continues to grow, but as this further extension does not primarily affect the placenta proper, it will be described elsewhere (see p. 468).

Concomitant with this growth of the allantois is a change in the general form of the placenta.

Before the allantois establishes contact with the placenta, and before the foetal blood-vessels had penetrated therein, its shape resembles that of a bell (figs. 37, 38). Thereafter the placenta becomes flatter, and gradually assumes the shape of an umbrella. The thickness of the placenta is finally a little less than half its diameter (fig. 21). In a section through the centre, the placenta appears to be divided into two equal halves by the enlarged placental arteries on their way to the free surface (fig. 20). When viewed from the foetal surface, the prominent foetal blood-vessels may be seen arborising in a radial direction, while in the centre of the placenta a notable depression is evident; this corresponds to the place of the emergence of the main placental arteries.

From the time of the primitive streak up to the 13-somites stage, the growth of the placenta was maintained by a steady, almost unobtrusive,

proliferation of nuclei situated in the spongy layer immediately deep to the radial vessels. These nuclei proliferated and migrated steadily down and along the cords deeper into the spongy layer. At irregular intervals along these cords small clusters of nuclei could be detected. Even at the 13-somites stage there was no evidence to the effect that this proliferation was more active than at earlier stages. Up to this time, too, decidual emboli could be seen in the arcades as well as in the dilated venous sinuses deep down in the spongy layer.

Immediately after the allantois has established contact with the placenta, however, a remarkable phase of proliferative activity is initiated in a layer continuous over the whole embryonic surface of the placenta, immediately deep to the radial vessels. It is difficult to decide whether this proliferation occurred at first immediately underneath the site of first contact of the allantois or not, since in the 18-somites stage the allantois has already established contact with the placenta, and the proliferative activity has affected the whole extent of the zone interposed between the radial vessels and the spongy layer. This proliferative activity becomes progressively more intense, and reaches a climax at about the 30-somites stage, at which time the allantois has already spread right across the placenta. This intense mitotic activity is maintained unabated until the embryo has reached a length of 10 mm. In sections, this layer of proliferatic activity is conspicuous by the great density of the newly formed nuclei (fig. 20). Towards the embryonic side of the placenta it is sharply delimited, but it gradually merges into the spongy part. Except for the density of nuclei, this layer structurally is not different from the spongy part of the placenta.

Up to 12·5 mm. the zone of proliferation is still present, but when the embryo reaches a size of 15 to 18 mm., the active growth of the placenta decreases to such an extent that mitotic figures can no longer be observed; the proliferating zone as such has disappeared completely, and is incorporated in the spongy layer.

The result of the mitotic activity in the zone of proliferation is twofold: in the first place, the spongy part of the placenta is rejuvenated; in the second place, a completely new part is added to the placenta.

This proliferation is associated with a steady migration of nuclei within the cords of the spongy layer. In the zone of proliferation the nuclei are embedded in cytoplasm, in which no intercellular membranes could be identified by means of the several techniques that have been used for the purpose. Already by the 30-somites stage the nuclei have begun to move progressively from the proliferative zone into the cords of the spongy layer. This migration occurs most actively down the cords related to the central placental arteries, and here they penetrate most deeply into the

spongy layer. The depth of penetration of these nuclei becomes progressively reduced towards the periphery of the placenta.

This steady influx of nuclei into the spongy layer extends in depth until the whole of the spongy layer has been pervaded; the rows of newly formed nuclei may be seen throughout the entire layer. This process of migration of the nuclei is much more intensive in the centre along the uterine arteries and, by the time the embryo has reached the size of 40 somites, they have penetrated the whole central part of the placenta and are spreading out even in the decidua.

At this time, too, the periphery of the placenta has now become involved. By the time the embryo is 4·9 mm., the whole of the spongy layer has become revitalised by this enormous accession of nuclei from the zone of proliferation. Once these nuclei begin to move from the zone of proliferation in the direction of the spongy layer, mitosis is completely inhibited. In the zone of proliferation, however, not only is there a superabundance of mitotic activity, but also grossly abnormal mitotic figures have been repeatedly detected.

With the migration of the nuclei into the cords of the spongy layer, there is a reduction in size of the nuclei associated with a great accumulation of chromidial substance in the cytoplasm, so that in some areas robust rodlets of chromidial substance become arranged around the periphery of the nuclear clusters. The new nuclei are formed at such an enormous speed that they distend the cords and form projections into the placental lacunae. These outgrowths become pedunculated, and finally break off to lie loosely in the blood-channels. Soon after this severance the nuclei undergo karyolysis. The proliferation is so active, however, that karyolysis may even occur irregularly in the zone of proliferation itself. The great proliferation of nuclei, and their migration into the contiguous cords of the spongy layer, leads first of all to a great thickening of the individual cords, and then to a straightening out of these cords. As a consequence, the broad nucleated cords, in contact with the zone of proliferation, seem to alternate regularly with the placental lacunae. The cords and the lacunae, however, become more sinuous towards the region of attachment of the placenta. Later, however, the cords of the spongy layer become increasingly narrower and at the same time more numerous. Also the vascular channels between the cords carrying the maternal blood become narrower and increase in number (figs. 18, 19, 20, 21).

During the period of migration of these nuclei the cell membranes in the cords are grossly modified or even destroyed, for in no other way is it possible to explain this remarkable migration of the nuclei. At an earlier stage, before the allantois establishes contact with the placenta, the cell membranes, although very delicate, could nevertheless be recognised.

After the migration of nuclei the ectoplacenta is formed by a syncytium, and it remains a syncytium until the end of pregnancy. The factors responsible for the dissolution of the cell membranes remain a mystery. If the membranes between the adjacent cells are dissolved, by contrast, the membranes of the cells directed towards the lacunae maintain their robust character.

During the phase of nuclear migration, the cytoplasm forms a tight sleeve over the rows of nuclei which in turn are arranged as a central core in the cords. The emphasis at this stage is undoubtedly on nuclear proliferation and migration.

Nuclear degeneration is a frequent event and takes place in one or two ways: viz. by reduction in size and loss of nuclear detail associated with heavy staining, or by an enlargement of the nucleus and a loss of chromatin material until all that remains of the nucleus is a nearly empty vesicle. The former degenerative process usually involves the clusters of nuclei, whereas the latter is more commonly encountered in the dispersed nuclei.

It is noteworthy that, prior to the initiation of active proliferation and nuclear rejuvenation of the spongy layer, the abundant red granules, noted previously up to the 13-somites stage in the cytoplasm of the spongy layer, rapidly disappear as soon as mitosis sets in. Moreover, it might be mentioned that, whereas emboli of decidual cells could frequently be seen caught in the lacunae of the spongy layer, soon after the allantois establishes contact with the placenta these emboli disappear completely, despite the intensified destruction of the decidua and of the small veins lying therein. This aspect of the problem will receive further examination at a later stage (see p. 483).

The large number of nuclei packing the cords of the spongy layer at an earlier period are reduced by massive destruction and by karyolysis of individual nuclei. The net result of this nuclear destruction is a great reduction in the number of nuclei per unit area. By the time the embryo has reached a size of 18 mm., the nuclei are for the most part regularly spaced throughout the spongy layer except for a small zone near the attachment of the placenta to the uterus. Mitotic figures no longer occur in the ectoplacenta after the 18 mm. stage, and it can thus be regarded as fully stabilised. The broad features of the ectoplacenta at 18 mm. are no different from those observed in the uterus when the embryo has reached a length of 38 mm., that is a little while prior to parturition.

The most striking result of the activity in the zone of proliferation, that was itself initiated by the allantois making contact with the placenta, is the addition of a completely new part to the placenta.

The foetal vascularisation of the placenta is dependent, in the first instance, on the proliferation of the mesoderm and its insertion between the radial maternal vessels lined by trophoblastic epithelium. As already

mentioned, the mesoderm initiates this process almost immediately after the allantois has touched the placenta (fig. 46). Delicate strands of mesoderm cover the arcades formed by the radiating branches of the placental arteries, and insert themselves in the angles between adjacent arcades. It must be remembered that the trophoblastic epithelium, enclosing the radiating branches of the artery, is well differentiated, and mitotic figures are only rarely encountered in this region. But active growth takes place immediately below the radiating vessels. For this reason it becomes evident that the penetration of foetal blood-vessels is materially facilitated by active growth of the ectoplacenta, which expresses itself by a shifting of the radiating vessels in the direction of the uterine cavity. Simultaneously, the mesoderm inserts itself between these vessels. As a consequence, the vessels become more and more separated and, to a lesser extent, slightly pedunculated (fig. 38).

The differentiative processes in the placenta manifest themselves mainly by the addition of a completely new layer to the placenta which, on account of its appearance, can be designated as the columnar layer. It is intercalated between the more and more protruding radiating vessels and the zone of active proliferation. The spongy part of the placenta, on the other hand, does not change its structure, and no allantoic tissue, carrying embryonic blood-vessels, will penetrate into it. Thus there is more reason for taking this process as a penetration of the trophoblastic tissue into the substance of the allantois.

By the time the embryo has formed 27 somites, not only is the placenta completely covered by the allantois, but shallow vascular channels, filled with embryonic blood, pass as wide loops from the allantois into the newly added superficial parts of the placenta (figs. 47, 48). Further, the distance between the branches of the radial vessels, filled with maternal blood, is increased. A narrow pedicle, continuous with the zone of active proliferation, supports these vessels; it consists of a type of differentiated epithelium similar to that enclosing the radial vessels. At irregular intervals the pedicle is traversed by branches of the radial vessels on their way through the substance of the placenta to join, ultimately, the placental vein (fig. 47).

The growth of the placenta, therefore, is made possible, on the one hand, by the continued proliferation of the ectoplacenta in the zone of active growth situated between the columns and the spongy layer, and, on the other hand, by a reciprocal proliferation of the allantoic mesoderm in contact with the chorion. In this way the size of the vascular bed of the foetal placental circulation is progressively increased. *Pari passu* with the lengthening of the columns, the allantoic capillaries between them elongate and the columnar layer increases in thickness.

Even at this early stage the allantoic mesoderm has differentiated into

endothelial cells enclosing the foetal blood. At the same time, the mesenchymal cells form reticular fibres and these encircle the foetal placental capillaries. The nucleated erythrocytes of the foetus can be detected lying in relatively dilated capillaries running between the short columns.

The complete differentiation of the placenta and the stabilisation of the foetal circulation is a gradual process. When the embryo is 7 mm. in length, and even at a length of 10 and 11 mm., growth of the placenta and the enlargement of the foetal capillary bed is still incomplete (fig. 20). The zone of actively growing ectoplacental tissue has not lost any of its vigour; mitotic figures are here abundant and the nuclei are crowded.

During the continued growth and expansion of the placenta, the pattern of the radial blood-vessels becomes more complicated by the addition of numerous side branches. Correspondingly the number of columnar capillaries steadily increases, and they may arise as branches of previously formed capillaries, or originate directly from a radial vessel. During this period, when there is a progressive increase in length, as well as in number of the individual columns, the radial blood-vessels become better defined as distinct entities, and gradually come to assume a position on, or even above, the inner surface of the placenta, where they lie alongside the main branches of the allantoic vessels.

By the time the embryo has attained a length of 18 mm. the placenta is fully stabilised, the proliferating zone has disappeared, and no further change in structure can be detected throughout the rest of pregnancy.

The Structure of the Definitive Placenta.—The general structure of the placenta at the 38 mm. stage is shown in fig. 21. The plane of section passes through the centre of the placenta along the axis of one of the placental arteries. From an examination of this figure it is evident that the placenta consists of three layers, viz. a prominent and well-differentiated columnar layer immediately related to the allantoic cavity, a broad spongy layer, and a very narrow anchoring layer.

Columnar Layer.—This layer comprises one-third to one-quarter of the placenta. It is uniformly thick except for the overlapping margin, where it is thinner, and for a tongue-like projection in the centre in relation to the placental arteries, where it may penetrate over almost three-quarters of the thickness of the placenta. The columns are composed of trophoblastic syncytium separating the maternal blood from the allantoic blood-vessels. The syncytium consists of a very much flattened plasmatic layer with large vesicular nuclei spaced at wide intervals. This syncytium is directly continuous with that forming the spongy layer, but the marked divergence in the structure of the two layers is so profound that, at low power, a sharp line separates the two layers (fig. 21). The maternal blood flows through the columnar spaces which are lined by this trophoblastic syncytium.

The allantoic blood-vessels, on the other hand, are lined throughout their course by an endothelium supported by a delicate reticular layer. These allantoic vessels extend to the junction between the columnar and spongy layers. For this reason, endothelial cells and the reticulum can only be seen in the columnar layer. It is certain that no foetal blood penetrates beyond the layer of columns into the spongy layer. This fact is clearly established by the delineation of the foetal blood-vessels in the young placenta which, at that time, are rendered conspicuous by the nucleated red cells and, in an older placenta, by the endothelium and the reticulum surrounding the allantoic vessels. From this it can be concluded that at least one-third of the placenta does not directly serve the foetal circulation. The maternal blood, derived from the placental arteries, enters the placenta via the narrow channels passing through the columnar layer and enters directly into the wider channels of the spongy layer (fig. 49).

After the embryo has passed the 10 mm. stage, larger allantoic vessels may be seen at irregular intervals coursing through the layer of columns. The direction in which the embryonic blood flows through the columnar layer will be described later (see p. 497).

Spongy Layer.—This layer, as already mentioned, comprises the greater part of the placenta. It consists of a maze of relatively broad cords which are continuous with the much narrower and regularly arranged columns. The cords of the spongy layer converge towards the narrow placental peduncle.

The cords consist of a syncytial layer with a prominent membrane bordering on the blood spaces. The thickness of the cords is slightly more than the diameter of the nuclei. The latter are regularly spaced; they have a prominent nuclear membrane enclosing coarse clumps of chromatin. The cytoplasm, in haematoxylin and eosin preparations, contains fine eosinophilic granules which also stain with Scharlach. On the whole, the calibre of the blood spaces in the spongy layer is rather uniform, but as the cords converge towards the zone of attachment, the blood spaces become larger and sinusoidal in appearance.

Attaching Zone.—This zone is restricted to a narrow area related to the placental arteries and veins. As compared with earlier stages it is greatly reduced (*cf.* figs. 38, 21). Some of the nuclei of the spongy layer pass into the adjoining necrotic debris, which consists of inspissated secretion, the remnants of the uterine glands and of the necrotic decidual tissue. This tissue has a semi-solid consistency. The syncytium stops rather abruptly and, at the point of contact with the necrotic tissue, clusters of hyperchromatic nuclei may be seen demarcating the anchoring zone from the necrotic decidua.

This anchoring layer is pierced in the centre by the two placental arteries

and at irregular intervals by the placental veins. The wall of both these arteries and veins consists of a dense network of collagen fibres. The placenta is attached almost exclusively to the uterine wall by these collagen fibres of the thickened walls of the arteries and of the vein.

Summary of the Stages in the Placental Development.— From the foregoing it is evident that the formation, growth, and differentiation of the placenta may be conveniently, but arbitrarily, divided into six stages.

(1) Pre-implantation stage. This embraces the formation of the embryo-chamber in which the embryo is lodged and the polarisation of the blastocyst, so that the placental cap is defined in relation to the chamber epithelium, whereas the obplacental pole of the embryo, constituting the yolk-sac, enlarges to encroach upon the main uterine cavity.

(2) Penetration and necrosis of the chamber epithelium. From the placental cap the plasmoditrophoblast is rapidly differentiated. This syncytial mass, in the form of finger-like processes, penetrates the stratified necrotic chamber epithelium to broaden out against the basement membrane, providing in this way a temporary anchorage for the embryo.

(3) Formation of the primitive placenta. After the embryo is superficially attached to the chamber epithelium, the plasmoditrophoblast perforates the basement membrane and rapidly invades the depth of the decidua in the form of a few long root-like processes, which produce only limited, and very locally restricted, injury to the maternal tissues. These root-like processes now anchor the embryo more securely to the decidua. The cytotrophoblast, by digestion of the chamber epithelium and the basement membrane, follows in the wake of the plasmoditrophoblast and consolidates over a wider but shallower area the attachment of the embryo. By the formation of the primitive villi, derived from the cytotrophoblast, the dilated underlying maternal blood-vessels are opened and a primitive intervillous circulation is initiated.

(4) First phase of placental growth. Soon after the establishment of the primitive circulation, a demarcation between the placenta and the maternal tissues is tentatively effected by a reticulum enfolding the distal extremities of the cytotrophoblastic villi. Simultaneously, the long roots of plasmoditrophoblast atrophy and thereafter completely disappear. Further growth of the placenta now takes place almost exclusively in the direction of the uterine cavity. The lengthening of the villi results in the formation of a spongy mass of trophoblastic tissue, and defines the direction of the flow of the maternal blood through the young placenta. As a rule two unbranched maternal placental arteries penetrate through the centre of the placenta to reach the free surface of the placenta, where they divide into a number of radiating branches. The latter return via a number of

irregular lacunae in the spongy mass to be collected at the anchoring zone by several veins.

(5) Second phase of placental growth, and the development of the foetal placental circulation. When the allantois establishes contact with the placenta, a new phase of growth and differentiation is initiated. A columnar zone is added to the free surface of the placenta. Vigorous growth of the placenta is made possible by active mitosis in a layer located between the spongy and the columnar regions. The foetal blood-vessels penetrate into the layer of columns only. In this way the fundamental plan of the fully formed placenta is determined.

(6) Complete stabilisation of the placenta. With the cessation of growth and the complete differentiation of the columnar layer, the placenta has reached full maturity.

The destruction of the decidua and related glands fixes permanently the utero-placental junction, and the only attachment of the placenta to the uterine wall is provided by the placental arteries and veins supported by a fibrous sheath.

With the disappearance of the zone of proliferation, the columnar and the spongy layers become apposed, and are sharply demarcated from one another.

The Embryonic Membranes.

In *Elephantulus* the trophoblast differentiates late as compared with other placental mammals. As a consequence the yolk-sac is formed almost simultaneously with the trophoblast. This is followed, almost immediately, by the appearance of the amnion, and only much later does the allantois obtrude itself as a distinct entity.

Since the yolk-sac and the allantois play an important part in foetal nutrition at consecutive stages in development, it will be necessary to consider these structures in some detail. For the sake of completeness we wish to make a few comments on the amnion.

The Amnion.—As the amnion is formed by cavitation, it can be recognised at a very early stage (fig. 31), and the amnio-embryonic vesicle is a distinctive feature at the time of the formation of the trophoblast and before the embryo penetrates into the maternal tissues. At first this vesicle is not polarised, but as soon as it reaches the region of the placental cap, the thicker embryonic part of the vesicle can be recognised as distinct from the thinner amniotic roof (fig. 40). Coincident with this polarisation the plasmoditrophoblast has invaded the decidua. With the steady increase in size of the amniotic cavity the ectodermal layer of the amnion becomes progressively thinner, and more sharply delimited from the embryonic ectoderm.

The distinct pro-amnion surrounds the whole of the head region at an early stage (fig. 44); it is still seen at the 34-somites stage, and it may persist even for a much longer period.

The Yolk-Sac.—As previously described, the embryo arrives at the implantation site in the four-celled stage. Thereafter the blastomeres start to proliferate vigorously to form a vesicle, lined by a single layer of cells. This vesicle completely fills the embryo-chamber (fig. 24). Only a very small part of the surface of this vesicle is not in contact with the chamber epithelium, and is exposed to the lumen of the uterus. From the whole wall of this vesicle cells are detached, and they concentrate at first as a solid ball, which later develops a cavity in the centre. This ball is now the amnio-embryonic vesicle and it lies free within the larger trophoblastic vesicle, usually called the segmentation cavity. The continued proliferation from the inner aspect of the wall of the outer vesicle results in the appearance of cells which eventually cover the amnio-embryonic vesicle, and further arrange themselves as an inner lining to the outer epithelium, which can now be regarded as trophectoderm. This new inner layer constitutes the entoderm and, together with the trophoblast, forms a bilaminar yolk-sac.

Coincident with the formation of the bilaminar yolk-sac, the primitive placenta differentiates from that part of the wall of the original blastula which was in contact with the epithelium of the embryo-chamber. By contrast, the very small part of the blastula, not in contact with the chamber wall, eventually forms the large yolk-sac. In the early stages, therefore, the yolk-sac is very small as compared with the relatively large placental cap. Later, the yolk-sac enters a phase of extremely active growth and, as a consequence, it protrudes through the neck of the embryo-chamber to encroach upon the main uterine cavity. This growth of the yolk-sac is demonstrated in figs. 9, 10, 11, 12.

During the primitive streak stage the bilaminar yolk-sac reaches its peak of development, completely filling the bursa embryonica (fig. 14). By comparison the placenta now forms only a small cap, in extent about one-fourth of the circumference of the yolk-sac. In the early primitive streak stage the mesoderm starts to penetrate between the outer and inner layers of the bilaminar yolk-sac (fig. 37). By the time the embryo has developed five somites, the primitive yolk-sac blood-vessels may be identified in the splanchnic mesoderm. These vitelline vessels penetrate steadily between the ectoderm and entoderm; at the 13-somites stage they extend over two-thirds of the circumference of the yolk-sac, after which time further advance is greatly retarded. Nevertheless, complete vascularisation of the yolk-sac occurs before the yolk-sac shows any signs of degeneration (fig. 18).

After the 13-somites stage the yolk-sac no longer increases in size, and

the continuous enlargement of the bursa embryonica is mainly effected by the rapid growth of the embryo itself (*cf.* figs. 15, 18). Throughout the whole of its development and more particularly after the bursa embryonica has formed, the large yolk-sac is in intimate contact with the actively secreting bed of uterine glands, which is responsible for the formation of the decidua pseudocapsularis. This intimate relationship is largely responsible for the nutrition of the embryo, until such time as the allantois makes it possible for the foetal vessels to use the placenta as a source of nutriment.

By the time the amnio-embryonic vesicle has reached the placental pole, and the investment of the trophoblast by the entoderm has been completed, the yolk-sac is already a very large structure. At this stage the wall of the yolk-sac is in broad contact with the primitive placenta (fig. 35). With the formation of the amnion and the development of the mesoderm, the extra-embryonic coelom then makes its appearance. This extra-embryonic coelom progressively reduces the area of contact between the yolk-sac and the placental surface (fig. 37). Eventually the yolk-sac becomes completely separated from the placenta (fig. 15).

During the growth of the yolk-sac small ectodermal papillae may be seen scattered irregularly over its surface. As a rule these papillae coincide with the orifices of the uterine glands. Occasionally, however, these papillae have no relation to the glands. The histological appearance of the papillae is reminiscent of similar structures occurring in the large yolk-sac of the pig. In these papillae mitotic figures are often seen, so they may be considered as a focus of growth.

This very large yolk-sac serves as a mechanism for nourishing the embryo during its early stages of development.

The Allantois.—As previously mentioned, despite the fact that the placenta is a very large structure, the embryo does not take direct advantage of this mechanism for sustaining itself until the 18-somites stage is reached. The only connection between the embryo and the placenta before the 18-somites stage is provided by the *a*-vascular chorion (fig. 44).

The early developmental history of the allantois has already been described (van der Horst, 1944 *a*).

The allantois can be unambiguously recognised as a distinct entity in an embryo with five pairs of somites. Prior to this stage, the lumen is represented by a small indentation in the mass of cells, connecting the posterior end of the embryo to the chorion. This mass consists of mesodermal cells, and has been identified as a connecting stalk. In the average embryo of *Elephantulus* some doubt may exist as to the nature of this mass of mesodermal cells, but in the unusual circumstances where the embryo had completely embedded itself in the decidua, no doubt can be raised about

the nature of this cell mass. It conforms to the criteria generally considered as applying to a typical body-stalk as formed in man and monkeys (van der Horst, 1947).

In the average embryo the indentation of the connecting stalk becomes deeper, carrying the thick mass of mesoderm in front of it. In an embryo with 12 somites it appears, therefore, as a little sac with a thick wall hanging down into the extra-embryonic coelom like a short tail. At the 14-somites stage, as shown in fig. 44, the dorsal aspect of the embryo is in apposition to the free surface of the placenta, with the already vascularised allantois protruding from the ventral surface of the embryo into the exocoelomic cavity. Between the 14- and 18-somites stages of development a remarkable series of events is enacted (*cf.* figs. 44 and 45). Firstly, the greatly enlarged and richly vascularised allantois establishes contact with the placenta, and secondly, this swinging round of the allantois from a ventral to a dorsal position is accompanied by a corresponding rotation of the tail end of the embryo, so that the side of the embryo now abuts against the free surface of the placenta. This rotation of the embryo advances cranially until the whole embryo lies on its side (fig. 18).

The rotation of the allantois, as well as the addition of 4 somites, from 14 to 18, to the embryo, appears to be a rapid process, as, notwithstanding the size of our collection, all efforts to fill in this gap of critical stages have not been successful. The sequence of events culminating in this remarkable phenomenon still remains to be investigated. At any rate, the contact of the allantois with the placenta constitutes a landmark of the utmost importance.

Once the allantois has established contact with the placenta a new phase of growth of the placenta is initiated, which culminates in the complete maturation and stabilisation of the placenta (see p. 457).

At first the allantois has the form of a slightly curved cylinder (fig. 45). Consequently, in the 18-somites stage only a small area near the centre of the placenta comes in contact with the allantois. At this stage the allantois has a small lumen enclosed by a thick wall.

Thereafter two main events can be recognised in the later developmental history of the allantois. The first relates to the integration of the foetal and maternal circulation, made possible by the establishment of an intimate connection between the allantois and the placenta. The second concerns the repercussions of the secondary enlargement of the allantois on the structure and destiny of the yolk-sac.

The first event has two attributes, namely, the spreading of the allantois over the entire free surface of the placenta, and the interlocking of the allantoic vascularised mesoderm with the outgrowing columnar layer of the placenta, through which the maternal blood circulates.

When the allantois spreads out over the placenta its attached side remains thick, while the side facing the embryo becomes greatly attenuated (fig. 38). When the whole of the placenta is covered, which happens at the 25- to 27-somites stage, the embryo is attached to the placenta by a very delicate allantoic membrane, enclosing the engorged allantoic blood-vessels. Simultaneously with the spreading out over the placenta, the allantoic mesoderm, carrying with it the foetal blood-vessels, interlocks with the developing columnar layer of the placenta as previously described (see p. 461). In this way the foetal and maternal parts of the placental circulation are now integrated.

The second event in the allantoic development is enacted shortly after the whole free surface has been covered and vascularised by the allantois. In the 30-somites stage the allantoic mesoderm begins to concentrate in the angle between the exocoelom and the periphery of the placenta (fig. 17). Soon thereafter a small veil-like diverticulum of the allantoic cavity descends along the whole circumference of the chorion. Such a diverticulum is portrayed in fig. 18. This narrow outgrowth gradually wedges itself between the chorion and the yolk-sac. The latter is now progressively separated from the superficial chorionic epithelium which lies in apposition to the wall of the bursa embryonica. The continued penetration of this circular allantoic outgrowth finally separates the yolk-sac completely from the chorion (fig. 19).

As a consequence, the yolk-sac becomes reduced in size (*cf.* figs. 15, 18, 19). Moreover, the original flat entodermal epithelium of the yolk-sac gradually becomes transformed into an epithelium, at first consisting of low cuboidal and later broad columnar cells. The yolk-sac, thus removed from the uterine wall, no longer seems to participate in nourishing the embryo, and its function has been supplanted by the allantois. Up to the 18-somites stage, at least, the nutrition of the embryo is mainly dependent on the functional activity of the yolk-sac. Between the 18- and 25-somites stage the allantois begins to participate in the nourishment of the embryo, and for a transitory period, from the 27- to about the 40-somites stage, the rôle of the yolk-sac is progressively eclipsed. During this period of transition, both the yolk-sac and the allantois provide the nourishment for the embryo.

The Rudimentary Secondary Placenta.—As long as the decidua pseudocapsularis intervenes between the bursa embryonica and the main uterine cavity, the chorionic ectoderm, covering the yolk-sac, remains a thin membrane, consisting of a single layer of flat epithelium (figs. 15, 50). Even after the allantois has established contact with the placenta and has commenced to insinuate itself between the yolk-sac and the chorion, there is still no change in this chorionic epithelium (fig. 51). However, by this time the trilaminar yolk-sac begins to protrude through the communication

between the bursa embryonica and the main uterine lumen (fig. 17). It is at this stage too that the incipient degenerative changes can be detected in the decidua pseudocapsularis. As the further enlargement of the uterus is confined, henceforth, exclusively to the area of the antimesometrial pole, the main lumen of the uterus in this region becomes correspondingly dilated.

The continued enlargement of the uterus, associated with the degeneration of the decidua pseudocapsularis, results in a great increase in the diameter of the communication between the bursa embryonica and the main uterine lumen. At this time the conceptus begins to alter its shape from a hemisphere to a sphere (see fig. 1). With the opening up of the communication the embryonic membranes enter the main uterine cavity. It will be recalled that, while these events in the bursa embryonica were being enacted, the allantois had already spread out to cover the yolk-sac completely. The related chorionic epithelium is now in contact with the allantoic mesoderm. This process has, as a consequence, a switch from a yolk-sac to an allantoic circulation. While the main allantoic circulation is undoubtedly concentrated in the placenta, nevertheless a significant part of the allantoic circulation is diverted to the obplacental part of the chorion (fig. 19).

With the widening of the communication between the bursa embryonica and the main uterine lumen, the chorion with its newly acquired allantoic blood-supply establishes intimate contact with the hitherto apparently inactive epithelium of the obplacental pole of the main uterine lumen. This new relation, between the embryonic membranes and the hitherto unaltered uterine wall, is associated with a profound change in the chorionic epithelium. Whereas the epithelium, coextensive with the old bursa embryonica, retains its simple character, the part of the chorion now protruding into the widened main uterine cavity becomes remarkably stratified (figs. 19, 52).

This transformation of the chorion is enacted very rapidly. When the embryo is 4·9 mm. long, this thickening cannot yet be detected (figs. 18, 51), but it is already very obvious in an embryo measuring 5·4 mm. (fig. 52), and is even more accentuated when the embryo has reached a length of 6·1 mm. (fig. 19). However, this unmistakable thickening of the chorionic epithelium is ephemeral; by the time the embryo is 7·2 mm. long a thinning is already manifest, and at the 8·2 mm. stage the chorionic epithelium is reduced once more to a single layer of cells (fig. 53).

Although this obvious modification in the chorionic epithelium is only transitory, it is nevertheless very significant in so far as it may be regarded as a rudimentary secondary placenta.

This latter view is put forward for the following reasons:—

(1) The thickening of the chorion occurs only when a contact is established between the allantois and the chorion.

(2) The allantois, in contact with this area of the chorion, is richly vascularised; these allantoic vessels continue to enlarge, and remain prominent throughout the transitory period of the thickening of the chorion.

(3) Although the allantoic vessels run for a considerable distance from the placental region to the obplacental side, the chorionic epithelium reacts only in a circumscribed, obplacental area.

(4) This area of thickening is confined to that part of the chorion which has established a new contact with a part of the endometrium, hitherto unaltered and separated from the embryo by the decidua pseudocapsularis.

Although this true, but rudimentary, placenta, with its stratified epithelium, has only a transitory existence, the chorionic epithelium related to the main uterine cavity, after being reduced to a single layer of tall columnar cells, retains a type of structure which is indicative of continuous physiological activity (fig. 53). These tall cells stand in contrast with the chorionic epithelium related to the degenerated remnants of the bursa embryonica.

The trophoblast as a whole can be divided into three main regions, viz.:

(1) The part which has constituted the placenta.

(2) An obplacental region consisting of regular, tall columnar cells.

(3) An intermediate region, related to the original bursa embryonica and consisting of an irregular epithelium, formed by cells varying in size and shape, many of which exhibit evidence of degeneration.

The chorionic epithelium, in the obplacental region, appears to maintain its activity until the embryo has reached a size of well over 12 mm. Thereafter, its general appearance becomes similar to that found in the intermediate region mentioned above.

Once the yolk-sac has ceased to be an intermediary in transporting nutrition from the mother to the embryo, its function is taken over completely by the allantois. Although the embryo is then nourished by the allantoic mechanism, it nevertheless receives its nutrition in two different ways during the first half of pregnancy. In the first instance the main placenta is the dominant organ, but this is supplemented by the obplacental area, which continues to transmit to the embryo the products derived from the uterine glands, in the same way as did the large yolk-sac in the very early stages of pregnancy.

The Uterine Glands throughout Pregnancy.

The changing aspect of the uterine glands during pregnancy can be considered conveniently under three main headings, viz:

(1) The changing form of a uterine gland during pregnancy.
(2) The pattern of reaction of the glands in the different parts of the uterus.
(3) The cytology of the glandular epithelium.

The Changing Form of a Uterine Gland during Pregnancy.—During the reproductive cycle, the glands in *Elephantulus* exhibit a remarkable series of morphological changes. In anoestrus, the simple gland is short and straight (fig. 54); in the early stages of oestrus, the proliferation of the cells leads to an increase of the girth and a threefold lengthening of the gland, and, as a consequence, the gland becomes coiled at first and then straightens out (fig. 55).

From the time of ovulation until parturition, the glands exhibit a regular pattern of reaction characterised by growth, differentiation and destruction.

When all the eggs are accumulated in the tubal egg-chamber, are fertilised and then start their descent through the Fallopian tube and the uterus, the long and straight glands, found at the time of ovulation along the whole circumference of the uterus (figs. 3, 56), become reduced in size. The dilated lumen, so conspicuous during the oestrogenic phase, now becomes narrower over its greater length, except for a restricted segment in the fundus. Mitotic activity in the glandular epithelium is sharply reduced. The oedema of ovulation is absorbed, and is replaced by a dense stroma which obscures, to some extent, the configuration of the glands (fig. 4).

In general it may be stated that, after ovulation, irrespective of whether it is sterile or fertile, the uterus passes into the stage of early dense stroma. It is thus apparent that after ovulation, for a short while at least, it is impossible, from an examination of the uterus only, to decide whether the animal is pregnant or not (van der Horst and Gillman, 1942 *a*, 1942 *b*). Therefore, it is likely that the embryo itself excites the specific reactions within an apparently sensitised uterus. Gérard (1923) states that the first transformation in the uterus, characteristic of early pregnancy, occurs shortly after ovulation, when the fertilised eggs descend in the tube. However, in the first stage of pregnancy the endometrium retains the same thickness as opposed to the phenomenal hypertrophy characteristic of the following stages.

As soon as the embryo of four blastomeres has arrived at the presumptive site of implantation, the reaction of the glands to the presence of the embryo becomes observable. Coincident with the increase of the blastomeres

from four to eight, a recrudescence of mitotic activity occurs in the glands related to the embryo-chamber. The localised oedema of pregnancy, as well as the growth and differentiative processes, contribute towards the significant thickening of the endometrium at the mesometrial side of the uterus (fig. 5). Soon thereafter the glands differentiate a narrow neck, a long dilated body and an unmodified fundus (figs. 5, 57). The appearance of the uterine glands towards the termination of this stage is shown in fig. 6.

The characteristic feature is the dilatation of the middle part, involving about three-fifths of the total length of the gland, while the neck remains relatively straight and the fundus unaffected. The dilated part of the gland assumes, more or less, the form of a corkscrew (fig. 57).

Although some uteri appear to be more sensitive than others, in general the degree of development of the uterine glands, prior to the stratification of the chamber epithelium, is of the same order. Some glands may be a little more coiled or a little more ballooned than others.

When the chamber epithelium has become stratified and the embryo has about 16 blastomeres, a wave of mitosis spreads over the whole length of the gland, involving even its deepest part. The distal third of the gland becomes extremely tortuous and zigzagged, communicating, on the one hand, by a short straight segment with the uterine cavity via the chamber, while on the other hand it opens out into a large ballooned segment. The latter in turn is continuous with the unaltered fundus. A reconstruction of the gland at this particular stage is portrayed in fig. 58. The lumen of the ballooned part subsequently becomes more regularly spherical and widely distended, but remnants of the original corkscrew are still evident. This part is a characteristic feature of a cross-section through the uterus at the site of implantation. It occupies approximately the inner half of the endometrium and extends close to the myometrium (fig. 6). For these several reasons the endometrium seems to contain many more glands than in the previous stage; in reality the number of glands does not increase.

The active proliferation of cells leads to a great increase in the length of the gland. This is associated with an exaggeration of the spirals in the distal half, together with an enlargement of the ballooned segment (figs. 7, 8). When the endometrium, and in particular the decidua compacta, increases in thickness, the glands become greatly elongated and the coils are partly straightened out. At this stage the gland has a striking appearance (fig. 59), and consists of four parts, viz. a straight, relatively short neck, an unaffected fundus, which is continuous with an enormously ballooned segment. The latter merges with a slightly coiled and slightly dilated distal part of the body, which is the largest part of the gland and corresponds with the tortuous segment represented in figs. 7 and 58. The coils are opened and, at the same time, there is a slight widening of the lumen.

As the lumen passes into the straight neck it becomes progressively narrower, till it joins a small crevice at its entry into the uterine cavity.

When the embryo is in the early blastocyst stage and the wall of the embryo-chamber shows definite signs of necrosis, the uterine gland, related to the chamber, has proceeded so far in its transformation that its further development is already clearly indicated (fig. 9). By this time the decidual reaction has progressed considerably; a dense mass of cells surrounds the embryo-chamber and, towards the periphery, this mass gradually changes into an oedematous tissue. The ballooned segment of the gland is now greatly distended, so that these parts of adjacent glands come in closer proximity to each other, reducing in this way the oedematous endometrium to narrow strands of tissue. These strands can be designated as the interglandular septa.

More striking is the metamorphosis of the originally large, corkscrew-like part of the gland that opened by a short neck into the embryo-chamber (fig. 58). In fig. 59 it is shown that this part becomes differentiated into two sections. Towards the periphery, and adjoining the balloon, the coils are retained and even accentuated, whereas the rest, towards the neck, straightens out. At the stage shown in fig. 9 this differentiation has progressed considerably. By a great distention, and a flattening in the radial direction, the spiral is now in its most conspicuous form. The straightened-out section, on the other hand, is narrowed to a thin tube that can no longer be distinguished from the previously short neck; this means that the neck is now long.

A result of this metamorphosis of the glands is the differentiation of the endometrium into two parts. In the centre, surrounding the embryo-chamber, the decidua compacta is traversed by the long, narrow necks of the glands. Towards the periphery the swollen glands progressively reduce the endometrium to narrow strands of tissue, and thus define the decidua spongiosa (fig. 9). Although the glands assume a more complicated form, the ramification, mentioned by Gérard (1923), never occurs in *Elephantulus*. Neither do the glands increase in number.

The further transformation of the uterine gland is a rapid process, as can be appreciated by comparing figs. 9, 10, 11 and 12. And fig. 60 depicts a wax-model of a gland at a moment when the embryo is hardly older than that of fig. 9 and younger than that shown in fig. 10. The delicate strands of tissue, or interglandular septa, were also found by Gérard (1923) in *Nasilio*. These layers of stromal tissue, on the one side, gradually increase in thickness as they merge with the deeper part of the decidua compacta, and, on the other, become very delicate where they become continuous with the connective tissue of the muscularis (fig. 61). Here the layers of tissue, separating the previously ballooned segments of the glands, become so

delicate that the peripheral walls of the several flattened glands collectively appear to form a continuous lining of tall epithelium to the inner aspect of the muscularis (fig. 11). This stromal framework between the distended glands supports the blood-vessels as they follow their tortuous and complicated pathway to and from the embryonic site (fig. 68).

Throughout this period of development it is apparent that, if the size of the glandular bed is any indication of activity, then it follows that the uterine glands are extremely hyperactive, and undoubtedly play an important part during the critical time of early placentation.

The subsequent destruction of the gland, effected apparently by two independent mechanisms, occurs at two different periods in time. The first destructive change in the glands is already apparent prior to the establishment of contact of the allantois with the placenta, and can be seen when the embryo has developed 13 somites. In this instance, the degenerative processes are restricted to the deepest part of the gland and, more especially, to the delicate septa between adjacent glands as they pass on to the muscularis. The affected cells shrivel up and, prior to their disappearance, can be recognised only as a thin rim of cytoplasm hugging the small, pyknotic nuclei. This necrotic process affects as well the contiguous walls of the adjacent glands as the thin layers separating the distended coils of the same gland (fig. 62). In this way the complexity of the glandular pattern is simplified and the lumina of different glands become confluent. Although a considerable amount of tissue is destroyed in this way, and several layers have been completely eliminated, the joint lumen of the fused glands remains very narrow.

A more obvious necrosis of the glands occurs in relation to the second invasion of the trophoblast soon after the allantois touches the placenta (see pp. 456, 485). The immediate effect of this penetration is the destruction of decidual cells as well as the parts of the glands in the neighbourhood. At the same time, liquefaction of the deeper part of the decidua compacta implicates all the elements of the decidua compacta, except the wall of the main placental blood-vessels (figs. 15–21).

The result of this holocaust is a large cavity between the placenta and the muscularis. This cavity is filled with necrotic debris and coagulated stagnant uterine secretions. This necrotic mass is traversed by the large placental vessels (fig. 21). Only the peripheral wall of the original balloons, now forming a continuous layer in close contact with the muscularis, escapes this destruction.

The remarkable selectivity of the necrotising agents is clearly illustrated by the fact that, whereas the greater part of the glands, and related decidual tissue, is completely annihilated, the glandular cells lining the muscularis remain astonishingly vital, and apparently continue to secrete actively

throughout the remaining period of gestation. These cells, together with those of the inactive fundus, after parturition regenerate the glands and the lining epithelium of the cavum uteri.

The climax of the growth and secretory activity of the glands is thus reached immediately prior to the moment of allantoic contact with the placenta.

The Pattern of Reaction of the Glands in the Different Parts of the Uterus.— It has been shown on a previous occasion that the endometrium during the menstrual cycle does not exhibit the same intensity of reaction throughout its entire circumference and thickness (van der Horst and Gillman, 1941 *b*). In the menstrual cycle this differential reaction is best seen in the stage of polyp formation, when the transformation of the stroma and the glands is confined to the endometrium nearest to the mesometrial pole of the uterus. Once it has lost its oestrogenic oedema, the endometrium at the opposite pole seems to remain inactive.

In pregnancy this contrast in the behaviour of the endometrium is even more pronounced. The most sensitive part of the uterus is located immediately adjoining the embryo-chamber (figs. 5–12). In this region the glands are most sensitive, and show structural changes at a very early stage of pregnancy. On the other hand, scarcely any change can be detected in the glands lying in the lateral wall of the uterus (fig. 5). Soon, however, the lateral glands become involved gradually and progressively in such a way that those lying nearest the chamber are more markedly affected than those towards the antimesometrial pole (figs. 7, 8).

In the early stages the transition from one pole to the other seems to be gradual, but later it is quite clear that the endometrium, including the glands, can be divided into a reactive and a seemingly non-reactive part, both of which are sharply demarcated from each other (fig. 11). The non-reactive part, in transverse sections, is limited to a small zone, comprising about one-quarter of the whole plane of a section, and seems to be restricted to the antimesometrial pole (fig. 9).

When the glands related to the chamber are already becoming flattened, in the way described above, the laterally situated glands are showing evidence of early swelling (fig. 9). It should be mentioned at this juncture that the reaction in the lateral uterine wall never becomes as intense as in the region of implantation, and also bears a different character. Consequently, the decidua here has no compact layer and is almost completely spongy.

The structural modifications in the laterally situated glands are depicted in figs. 9–12 and 15. These modifications are destined to separate the part of the uterine cavity occupied by the embryo, which may be called the bursa embryonica, from the main uterine lumen. This bursa embryonica

is delimited by the placenta, the greatly drawn-out lateral walls and a decidua pseudocapsularis (fig. 15). The bursa communicates through a narrow channel with the main uterine lumen.

The formation of the bursa embryonica is achieved by a great elongation of the mesometrial and lateral walls of the uterus. During this process, the glands of the lateral walls are at first moderately dilated along their entire length. They do not at any stage show the spiral structure nor the localised ballooning, which is such a characteristic feature of the glands in the region of the embryo-chamber. Subsequently, the lateral glands become compressed and, by their lengthening, converge towards the uterine lumen well beyond the yolk-sac (fig. 10), and later cause the lateral walls to bulge forward in the lumen (fig. 14). In this way a dilated embryonic portion becomes more and more separated off from the main uterine lumen. With the further enlargement of the uterus, and the continued convergence of the mouths of the glands from the opposite walls, the bursa embryonica finally becomes clearly defined (fig. 15). As a result of this process, the glands situated both in the lateral walls and at the mesometrial pole form an almost spherical cushion surrounding the embryo (figs. 11, 12).

Two facts deserve special emphasis. The first is that the reaction of the glands starts at the mesometrial pole of the uterus, and from there spreads along the lateral walls in an antimesometrial direction, but to a certain well-defined level only. The second fact is that the glands related to the embryo-chamber react in a way different from those of the lateral walls of the uterus.

The bursa embryonica increases in size until the embryo is approximately 5 mm. in length. At this time the bursa has achieved its peak of development (fig. 18).

However, it is already evident that the trophoblast, covering the yolk-sac, has entered the communicating canal, and is now just protruding into the main uterine lumen. Once the trophoblast has entered the main uterine cavity, then the bursa embryonica again communicates widely with the main lumen (fig. 19). These remarkable changes take place during the short period when the embryo grows from 4·9 to 5·5 mm. in length. Henceforth the wall of the hitherto narrow main uterine lumen (fig. 17) will extend with the continued growth of the embryo (see p. 445), with the result that what remains of the decidua pseudocapsularis seems to shift in a mesometrial direction (fig. 19).

Later on the necrotic process, which is already well advanced in the subplacental region, involves the glands of the lateral wall, until finally these also disintegrate, except for a layer of glandular epithelium lining the muscularis, which is continuous with a similar layer derived from the glands related to the placenta (see p. 476). As a result of this reorganisation,

the embryo lies once more in the main uterine cavity, and a single layer of epithelium again lines the wide uterine lumen.

Whereas the emphasis in glandular reaction has manifested itself first at the mesometrial pole and later in the lateral walls of the uterus, the antimesometrial portion of the endometrium begins to modify the structure, acquired soon after ovulation, only when the decidua pseudocapsularis is destroyed, and the trophoblast is able to establish free contact with the epithelium lining the antimesometrial part of the uterine cavity. Mitotic activity is initiated here, the lining epithelium becomes at first corrugated, and thereafter papillary processes project into the uterine cavity (fig. 19). The surface area is enormously increased, and the shallow glands unfold and remain as open pits, continuous with the projecting surface epithelium.

It is noteworthy that during the first period of pregnancy the mesometrial pole of the uterus starts to react, followed by stretching of the lateral walls of the uterus with the growing embryo, whereas the antimesometrial side apparently remains inactive. The boundary between the reactive and inactive parts of the uterine wall is sharply demarcated by the emergence of the decidua pseudocapsularis. Suddenly, when the embryo is 5 mm. in length, this process is reversed. Henceforth the mesometrial side and the lateral walls do not show any further alteration, and the continued widening and distension of the uterus involves exclusively the antimesometrial uterine wall. The result is that, when the embryo has reached a length of 20 mm. and more, the original mesometrial side occupies a very small area only in the region of the much enlarged placenta, and all the rest of the enormously distended uterus is formed by the antimesometrial wall only (see p. 445).

The Cytology of the Glandular Epithelium.—In conformity with the modifications occurring in the general form of the gland, the cells also undergo profound changes in their structure.

Apart from the fact that the mesometrial glands react earlier, and always remain in advance of those in the lateral walls, the constituent glandular cells of both exhibit a similar sequence of behaviour.

For descriptive purposes we wish to divide the gland of the mesometrial or lateral walls into three parts, namely, the fundus, the spiral part, and that part of the glandular wall which later comes to line the muscularis, *i.e.* the peripheral wall of the balloon.

In fig. 63 are portrayed the successive modifications of the cells in these three parts of the gland during pregnancy, and also of the epithelium lining the antimesometrial wall of the uterus.

The epithelium of the fundus of the gland is considerably higher than elsewhere, and, although it becomes slightly lower, the cells hardly change their form during the successive stages of pregnancy (fig. 63, B, 1, 2, 3, 5).

In the spiral part of the gland, during very early pregnancy, slightly older than the stage shown in fig. 5, the cells are about cuboidal with large round nuclei. When this part of the gland distends, the epithelium flattens correspondingly, until it consists of very flat cells with small, compressed nuclei that hardly bulge the cell wall into the lumen of the gland (fig. 63, A, 1, 2, 3, 4). With the whole of the decidua this epithelium is finally destroyed.

The part of the body which lines the muscularis reacts in a different way (fig. 15). Up to the stage of ballooning of the gland, the cells of this epithelium, in conformity with the other cells constituting the wall of the gland, are cuboidal. This shape is maintained unaltered until the decidua compacta and spongiosa is destroyed. Thereafter the epithelium becomes taller, and the cells increase in size to become high columns. This shape they maintain during the remainder of gestation (fig. 63, C, 1, 2, 3, 4, 5).

Until the decidua pseudocapsularis is destroyed, the cells of the glands in the antimesometrial wall behave in a fashion similar to those of the fundus described above. With the unfolding of the bodies of these glands, the epithelium now comes to line the uterine cavity, and consequently the originally low cells are converted into tall columns, indistinguishable from those forming the new lining of the uterine cavity. Thereafter, with the increase in size of the conceptus, the cells in the antimesometrial pole gradually become cuboidal, and merge with the slightly taller cells in the lateral wall of the uterus (fig. 63, D, 1, 2, 3, 4, 5).

The Decidual Cells.

In distinction from the rest of the uterus, the decidua compacta and decidua spongiosa are characterised by the presence of decidual cells of various forms.

Although the antimesometrial wall of the uterus, as well as the greater part of the original lateral walls, exhibit great changes during the course of pregnancy, this does not find a corresponding expression in the composition and form of their cellular elements. Typical decidual cells are only present in the mesometrial wall of the uterus, which, however, greatly extends during the first part of pregnancy. As described in the previous chapter, the destruction of the decidua compacta becomes evident at a rather early stage of pregnancy, and it will continue for a considerable time, until practically nothing is left not only of the decidua but also of the originally lateral walls of the uterus. Therefore, first the formation and then the destruction of the decidua will be considered.

The Formation of the Decidua.—During anoestrus the uterus is greatly contracted, and the endometrium has a uniform, dark appearance (fig. 2).

It can be stated at once that there is no difference at all between a young female and one that has been pregnant during the previous season. This, of course, reflects on the endometrium only; the muscularis, and particularly the uterine arteries at the mesometrial side, show considerable differences (van der Horst and Gillman, 1946 *b*). That no difference in the endometrium can be observed is not surprising, as practically the whole of it is destroyed during pregnancy and remoulded after parturition.

The dark appearance of the endometrium in sections is the result of the great number of small nuclei uniformly distributed over the whole thickness and circumference. A homogeneous cytoplasm is present between the nuclei, and where the nuclei are further removed from each other, smaller or larger vacuoles, with thin strands of cytoplasm between them, are present (fig. 64, *a*).

At the time of ovulation the oedema is distributed all round the uterus (fig. 3) (van der Horst and Gillman, 1942 *a*). The stromal cells, and particularly their nuclei, are large (fig. 64, *b*). The vacuoles also have increased in size, giving the stroma a sodden appearance. Mitotic activity is very intense.

When all the eggs are assembled in the tubal egg-chamber, and they are there fertilised and begin their segmentation, the oestrogenic oedema gradually disappears, and the stroma once again assumes a dark appearance in stained sections. Yet this dark stroma is different from that seen during anoestrus; also the uterus retains the same dimensions it had during oestrus (fig. 4). The darkness of the stroma is caused by an enormous increase in the number of nuclei, and these nuclei are of the same size as during oestrus, and much larger than the stromal nuclei of anoestrus (fig. 64, *c*). Otherwise the general structure of the stroma has not changed from that during oestrus. Further, no differentiation of the cells can be observed, nor is there any difference between the mesometrial and the lateral and antimesometrial walls of the uterus.

Soon after the early embryo has arrived at the implantation site a new oedema appears which, however, is restricted to the mesometrial wall of the uterus (figs. 5, 6). Henceforward a marked difference between this wall and the lateral and antimesometrial walls becomes a striking feature of the pregnant uterus (van der Horst and Gillman, 1942 *b*). Even when, later on, the oedema spreads to the lateral walls, the fundamental pattern of the stroma remains unaltered here; only the vacuoles greatly increase in size. In the mesometrial wall the vacuoles at once become larger and, notwithstanding the vigorous mitotic activity, the nuclei are widely separated (fig. 64, *d*).

Starting just underneath the embryo-chamber, and gradually spreading towards the muscularis, the pregnancy oedema is replaced by a denser

tissue (figs. 7, 8, 9). The real decidual reaction, accompanied by a differentiation of the cells, has set in. When the embryo is in the early blastocyst stage, the decidua compacta is already well set off from the decidua spongiosa (fig. 9). The latter is still highly oedematous, and shows a structure as seen in fig. 64, *d*. In the decidua compacta the cells have become more plasmatic, and the majority of them have assumed a characteristic pear shape, with the nucleus lodged in the broad end (fig. 64, *e*, *f*). Scattered between them are some spherical cells with a homogeneous cytoplasm and an irregularly shaped nucleus; these cells are the earliest manifestation of the giant cells (fig. 64, *f*).

When the embryo is in the early primary amniotic cavity stage (fig. 10), the pear-shaped cells have become very numerous in the decidua compacta (fig. 64, *g*). The young giant cells are swelling up already and thus become a conspicuous feature in a section. Often they have an irregular nucleus, some may be binucleate. Their cytoplasm contains coarse granules and many small vacuoles. A clear zone with only a few delicate strands of cytoplasm may be present in the peripheral part of the cell. Distinct from the pear-shaped cell, the young giant cells have a well-defined cell membrane.

The pear-shaped cells become less regular in form when the embryo is in the late primary amniotic cavity stage (fig. 12). Several of these cells can be seen changing into early giant cells by swelling up and surrounding themselves with a prominent cell membrane. By now the pear-shaped cells have appeared also in the decidua spongiosa, although the tissue here is still more open, containing large vacuoles. Even some early giant cells may be found here.

Sometimes, although not often, a giant cell may be found in the process of mitotic division (fig. 64, *i*). The number of chromosomes then is very striking. According to Brenner (1946), the diploid number is 14, but, especially when on rare occasions a large giant cell divides, the number of chromosomes becomes really astounding.

During the period when the embryo is in the primitive streak stage the number of giant cells steadily increases and the individual cells become larger. Often the surrounding pear-shaped cells are pressed flat like an endothelium. In the later primitive streak stage (fig. 14) the number of giant cells in the decidua compacta may have reached its peak, although most of them have not yet reached their maximal size (fig. 64, *k*). The pear-shaped cells from which, at a previous period, the giant cells were formed have completely disappeared from the picture. Those that have not changed into giant cells, and these form the majority, have been transformed into angular cells, closely fitted together and with conspicuous cell walls (fig. 64, *k*). Most of these cells are highly vacuolated, but some contain coarse, round, eosinophilic granules in a homogeneous cytoplasm

These granules are larger, but otherwise resemble those present in the fully formed giant cells.

When the embryo has formed 13 somites, thus before the allantois has made contact with the placenta, the breaking down of the giant cells in the decidua compacta, and their removal by the blood-stream, is already in progress. A great number of these giant cells, in various stages of decomposition, are found at this stage trapped in the narrow blood lacunae of the placenta (fig. 64, *o*). Yet a good many of them are still present in the tissue, and even some that have not completely finished their differentiation. In the decidua spongiosa, on the other hand, the formation of giant cells proceeds unabated.

Before the giant cells have reached their final stage of differentiation, and several never reach that stage, they are spherical in form with a sharply defined cell wall (fig. 64, *l*). The granular, eosinophilic cytoplasm is concentrated in the centre of the cell in the region of the irregularly shaped nucleus. The peripheral part of the cell is highly vacuolated, thus creating the impression that the giant cell is lying in a lacuna. This outer clear zone, however, is indeed part of the cytoplasm, as could be observed at earlier stages (fig. 64, *g*, *k*). The large peripheral vacuoles often fuse to form a large fluid-filled space, surrounding the concentrated cytoplasm in the centre. The original cell membrane remains sharply defined, and the central mass of cytoplasm may form a secondary cell membrane. Inside this cell membrane the process of vacuolation may be repeated.

In its ultimate form (fig. 64, *m*) the giant cell also exhibits a system of peripheral vacuoles. The granular, eosinophilic cytoplasm forms a hollow sphere in contact with the two or more nuclei. The centre of this sphere is more lightly stained, so in a section the cytoplasm appears as a darkly stained ring surrounding a clear inner area.

In the decidua compacta the giant cells are more scattered, they are smaller in number, but larger in size than in the decidua spongiosa. In structure, however, there is no difference. This enormous accumulation of giant cells in the decidua spongiosa is very striking indeed (fig. 64, *n*).

Having followed the decidual reaction in its ascendancy, we can now divert our attention to the complete destruction of the decidual tissue.

The Destruction of the Decidua.—When the embryo is in the late primitive streak stage the decidua compacta reaches its climax of development (fig. 14). Although the decidua spongiosa is still not fully differentiated throughout its entire thickness, destruction of the narrow septa, attaching the decidua to the muscularis, is already well in progress by the time the embryo has formed 13 somites (figs. 15, 62). A first indication, foreshadowing the necrosis of the decidua compacta, can already be detected in the primitive streak stage, when the pear-shaped cells as such have

disappeared, having been transformed into highly vacuolated cells (fig. 64, *k*). When the embryo has developed 13 somites, many of the decidual cells are very hydropic, and in low-power studies are represented by clearer areas (fig. 15). Other cells, however, have retained their healthy appearance. By the time the allantois has established contact with the placenta (18-somites embryo), indisputable evidence is present of the onset of necrosis. The cells become enormously ballooned due to the enlargement and fusion of the peripheral vacuoles (fig. 64, *h*). The conspicuous cell wall is connected by a few strands of cytoplasm to the nucleus. The spaces between these strands are occupied by vacuoles. The nucleus has lost its chromatic appearance, although the nuclear membrane is still prominent.

While the hydropic type of degeneration is quite common, frequently the cells with their nuclei lose their differential staining reaction and shrink, with the result that a granular mass of tissue makes its appearance. In this mass only the outlines of the much reduced decidual cells can still be recognised. In this instance the degenerated decidual cells change into a rather dense mass, which is concentrated chiefly around the walls of the placental arteries. Lateral to the zone of necrosis the decidual cells become markedly reduced in size, associated with a complete disappearance of the giant cells from that region. The giant cells may degenerate *in situ* with the rest of the decidua compacta. A more striking method of removing the giant cells is by way of the decidual arteries. Already in the primitive streak stage, when these arteries still have their endothelium intact, it can be seen that the adjoining giant cells bulge forward into the lumen (fig. 65). Shortly afterwards they completely penetrate into the lumen of the arteries, where they show a tendency to arrange themselves along the wall (fig. 66). By their great volume these giant cells considerably narrow down the lumen of the artery, and may even block it up completely. Some of these giant cells are lying free in the artery and are taken by the blood-stream into the placenta, where they pass the wider channels but become lodged like emboli in the narrower channels in the top of the placenta (fig. 64, *o*). Probably all giant cells that have invaded the decidual arteries are finally caught by the blood-stream. Taking into consideration that the giant cells accumulate especially in the neighbourhood of the arteries, it is likely that the majority of the giant cells, both in the decidua compacta and in the decidua spongiosa, are removed in this way. This process starts in the decidua compacta near the attachment of the placenta, and from there it gradually spreads to the periphery. When the embryo is in the 18-somites stage hardly any giant cells are left in the decidua compacta, and the penetration of the giant cells into the arteries is well under way in the proximal region of the decidua spongiosa (fig. 66).

The formation of giant cells surrounding the arteries is not confined to the decidua compacta and spongiosa. As has been described before (van der Horst and Gillman, 1946 *b*), the decidual reaction continues along the artery upwards, first in the myometrium and then in the mesometrium (see fig. 20 at the base of the mesometrium). It is noteworthy that the giant cells around the arteries, in these parts where no destruction of tissue occurs, are not destroyed or removed by the blood-stream. They are changed *in situ* shortly before or after parturition, and help to build up the thick hyaline wall of the arteries, characteristic of animals that have been pregnant before (figs. 2, 4).

It will be recalled that the secondary invasion of the decidua by the trophoblastic syncytium was already initiated by the time the embryo had developed 40 somites (see p. 460). It would appear, therefore, that the cytolytic effect of the trophoblast is initiated not only at the places of direct contact with the decidua, but also some distance beyond it. The final destruction of the decidua is related in some way to the secondary penetration of the trophoblastic elements.

In the uterus, associated with a 44-somites embryo, the trophoblastic elements have penetrated well into the superficial part of the decidua compacta in close proximity to the arteries; all giant cells have disappeared; the surviving decidual cells are shrunken; the necrotic decidua forms an outer sheath to the arteries, and is separated from the lumen by the trophoblastic elements and a rather dense reticulum, which is continuous with the fibrous layer anchoring the placenta to the decidua. With the exception of the trophoblastic elements and surviving decidual cells which protrude into the lumen (see p. 496), the wall of the arteries is relatively *a*-cellular.

The destruction of the septa is much more extensive, so that the embryo with its placenta is suspended from the muscularis almost exclusively by the placental blood-vessels.

However, it should be added at this stage that the periphery of the placenta is still connected to the drawn-out endometrium in the lateral walls of the uterus. These lateral walls are continuous with the decidua pseudocapsularis (figs. 18, 19). The placenta, therefore, still has a dual attachment even at the stage when the embryo is 6·14 mm. in length, viz. by means of the placental vessels at the mesometrial pole, and to the side walls via the hypertrophied lateral parts of the endometrium.

As the invading elements of the trophoblast penetrate the decidua compacta, the latter becomes progressively destroyed together with the glands contained therein (see p. 476.) As a consequence, the decidua compacta becomes markedly reduced in thickness and the remnants thereof consist of a mass of coagulated gland secretion and cellular debris (fig. 20). This necrotic mass is traversed by the vessels going to and from the placenta.

The fibrous walls of the vessels are continuous with the fibres on top of the placenta as well as with the necrotic mass.

Even though the decidua compacta in the neighbourhood of the placental attachment has undergone extensive destruction, the decidual cells around the coiled arteries in the decidua spongiosa continue to differentiate, and reach the peak of development only when the decidua compacta is completely destroyed (fig. 19). The destruction of the decidua spongiosa is a much slower process. Even when the embryo is 12·5 mm. in length a great part of the decidual tissue is still present (fig. 20). It persists as long as the placenta continues to grow, as reflected by the presence of the dense zone of mitosing nuclei between the columnar and spongy layers. This dense zone has finally disappeared by the time the embryo is 18 mm. long, and even then remnants of the decidua are still visible in the lateral walls, but they are no longer present when the embryo is 22 mm.

While it might be claimed that the destruction of the decidua compacta, with the subjacent part of the decidua spongiosa, is mediated directly or indirectly by the penetrating trophoblastic elements, such an explanation cannot account for the tardy destruction of the more lateral parts of the decidua spongiosa and of the decidua pseudocapsularis. Some other factors, therefore, influence the vitality of these parts of the decidua. These factors may be in some way connected with the maturation of the placenta.

From the time the embryo reaches a length of about 20 mm. until parturition, the embryo with the placenta is lying free in the enlarged uterine cavity, suspended only by the placental blood-vessels. The wall of the uterine cavity now consists only of the muscularis lined by a regular layer of epithelium, consisting of columnar cells derived from the peripheral portion of the ballooned segments of the glands. Only in the antimesometrial region does the surface epithelium persist as a lining to the uterine cavity.

The Myometrium.

In the non-pregnant uterus the muscularis consists of an outer longitudinal and an inner circular layer. Both these layers are well defined and of equal thickness over the whole circumference, except near the median uterus, where the longitudinal layer becomes about twice as thick in an area restricted to the antimesometrial pole. Even in the pregnant uterus this antimesometrial thickening is well demonstrated.

The part of the muscularis, which is particularly implicated during the first period of pregnancy, is confined to the mesometrial half of the uterus (fig. 17). Like the decidual reaction, the muscularis is gradually involved over an area almost coextensive with the decidua pseudocapsularis (fig. 14).

Up to this stage the affected muscularis stops abruptly near the line of attachment of the mesometrium and on the opposite side of the uterus at a corresponding level (fig. 14). With the increase in size of the bursa embryonica, associated with a corresponding distension of the uterus, the area over which the muscularis becomes affected spreads out towards the antimesometrial pole (fig. 15). Later, with the disappearance of the decidua pseudocapsularis, the muscularis throughout the entire circumference of the uterus is now uniformly involved (fig. 19). Thereafter, up to parturition, no fundamental changes could be detected in the structure of the individual muscle-cells.

Throughout gestation the circular layer remains conspicuous in a cross-section through the centre of the conceptus, as a continuous, uninterrupted layer, irrespective of the distension of the uterus. The longitudinal layer, on the other hand, is dispersed into bundles as it passes over the swollen part of the uterus. In a cross-section, therefore, this longitudinal layer can only be seen at irregular intervals as very attenuated bands of muscle fibres. As a consequence, the circular layer comes in direct contact with the perimetrium.

In the early stages of pregnancy, the first noticeable reaction in the muscularis is confined to the layer of circular muscles. This expresses itself in the form of oedema, which involves the connective tissue enveloping the individual muscle-cells. Soon thereafter the muscle-cells increase in length, and distinct myofibrils can now be seen embedded in a clear sarcoplasm. At the same time the cell wall becomes much more robust. The nuclei, too, are much elongated, and have lost the highly chromatic appearance characteristic of the non-pregnant uterus. Although occasional mitotic figures in the muscle-cells were seen up to the stage of the primitive streak, it is evident that there is no great numerical increase in muscle-cells. The fact that, with the enormous swelling of the uterus, the muscularis is not greatly reduced in thickness, implies that at least the individual muscle-cells must have undergone a great hypertrophy and considerable lengthening. This can actually be observed, more especially as individual muscle-cells are never so sharply defined as they are during pregnancy. The hypertrophy of the muscle-cell expresses itself certainly by an accumulation of fluid in the sarcoplasm, and by the formation of prominent myofibrils, which can be seen extending over a considerable length of the cell.

In this connection, too, it might be added that the intercellular oedema and swelling of the reticular fibres are noteworthy. Later on decidual cells, which surround the myometrial arteries, by their enlargement, further separate the muscle-fibres into smaller bundles.

Although the longitudinal muscle layer is broken up into separate bundles, its component cells also undergo hypertrophy in much the same

way as the circular muscle-cells, except that in the former the hypertrophy occurs more tardily.

In passing, it should be mentioned that the perimetrium becomes noticeably oedematous in the early stages of pregnancy (fig. 9). This occurs in irregular patches, and is not of the same intensity in different uteri. This oedematous reaction is confined to the embryonic bulge in the uterus. The accumulation of a mucoid tissue strips the peritoneum from the muscularis.

The Uterine Blood-Vessels.

The uterine blood-vessels of *Elephantulus*, at least those directly related to the placenta, show a complexity that may not be surpassed in any other mammal. This concerns not only their course, but also their transformations during pregnancy. These vessels are intimately connected with the decidua compacta and spongiosa, the formation and dissolution of which have been described in a previous section (see pp. 480, 483). In the construction of the placenta the vessels also play an important rôle.

It is convenient to examine the vascular phenomena by adopting the following procedure: firstly, to describe the course of the decidual vessels from the time of fertilisation until the beginning dissolution of the decidua; secondly, to examine the terminal portions of the decidual arteries and associated veins in so far as they are involved in the construction of the placental circulation; thirdly, to record the reorganisation of the decidual arteries and veins in relation to the dissolution of the decidua; and finally, the stabilised placental circulation will be analysed.

The Vascular Pattern during the First Part of Pregnancy.—At the time of ovulation, the vessels in some series of sections of uteri were sufficiently distended to permit a glimpse of the course of the uterine circulation. In these series it is seen that as soon as the mesometrial artery enters the myometrium, it branches into a number of subsidiary arteries which ramify in the muscularis. From the latter small arteries, delicate branches penetrate the endometrium at numerous points along the whole circumference of the uterus. These provide the endometrium with a capillary network and, branching repeatedly, they follow, on the whole, a straight course in the direction of the uterine cavity. Unfortunately, in this sectioned material the venous circulation could not be satisfactorily established.

Soon after ovulation and fertilisation the endometrium becomes more compact, characteristic of the early dense stroma stage. The reduction in the calibre of the vessels now precludes any analysis of the circulation in sectioned material.

From the dense stroma stage onwards until the embryo has arrived in

the embryo-chamber, and there has continued its development until the 32-blastomeres stage, no change in the blood-vessels could be detected. It is only now that an indication of the vascular pattern, characteristic of the first part of pregnancy, can be detected. Whereas at the time of ovulation the arteries appear to be equally prominent throughout the entire circumference of the uterus, in the 32-blastomeres stage slightly distended capillaries obtrude themselves, but they are restricted to a region of the endometrium related to the chamber, which itself is lodged in the mesometrial pole of the uterus. Here the dilated capillaries appear to be distributed throughout the thickness of the endometrium. These capillaries, however, are still too small to allow a mapping of their course.

The capillaries gradually increase their girth to reach the status of vessels, which can be indisputably recognised, by the time the late blastocyst is eroding the wall of the embryo-chamber. It can now be realised that the distribution of these dilated vessels closely corresponds to that of the decidual reaction. Therefore they will be designated as decidual arteries and decidual veins respectively.

When the embryo passes through the blastocyst stage, the decidual vessels become more and more distended. By the time the primary amniotic cavity appears, they already form a striking feature in a cross-section of the uterus (fig. 10). Soon afterwards it becomes obvious that the swollen vessels are distributed over two separate areas (figs. 12, 35). A few vessels can be seen immediately underlying the necrosing epithelium of the chamber wall or between the early penetrating villi (figs. 29, 31, 32). It is these few vessels that will give rise to the vascular bed of the placenta. They are separated from the numerous vessels so conspicuous in the peripheral part of decidua compacta, and in the decidua spongiosa by an *a*-vascular area (fig. 12). At this stage, for the first time, it is possible in sections to map their circuitous course through the transformed endometrium, and through the muscularis into the mesometrium, and thus to distinguish between decidual arteries and veins.

The arterial pattern has been reconstructed in several embryos throughout pregnancy. From the time the vessels obtrude themselves, until the destruction of the decidua (see p. 483), there is no further modification in the vascular pattern, other than an increase in size and a slight simplification resulting from this enlargement. Thereafter, with the destruction of the endometrium, a new pathway is fashioned, and this persists unchanged throughout the remainder of gestation. Therefore it is sufficient to describe, as an example, the course and distribution of the decidual vessels at a moment when the embryo is in the primary amniotic cavity stage. A schematic and simplified projection of these vessels on a longitudinal section is shown in fig. 67.

As a rule, three decidual arteries contribute towards the formation of the placental arteries (see p. 492). To simplify description the course of one of them will first be described, and thereafter the integrated pattern of the three decidual arteries will be examined.

In the primary amniotic cavity stage of development the uterine artery enters the myometrium from the mesometrium and, embedded in the myometrium, it branches in the usual way. As mentioned previously, two sets of endometrial arteries arise from the arterial network in the myometrium. The first set remains small during pregnancy, and is distributed to the whole extraplacental part of the endometrium. The second and very specialised set, the decidual artery, alone participates in the placental circulation.

The most prominent segment of the decidual artery, at this stage, is to be found in the decidua compacta. In the decidua spongiosa the artery is also distended, but to a much lesser extent. The least obvious part of the decidual artery is to be found at its origin in the muscularis.

The site of entry of the decidual artery from the myometrium may be anywhere along the circumference of the embryo bulge, at the same distance from the poles as the site of attachment of the mesometrium.

The course of the decidual artery in the primary amniotic cavity stage in brief is as follows: immediately after entering the decidua spongiosa the decidual artery suddenly dilates and follows a meandering course through the decidua spongiosa, which itself has become greatly distorted by the enlarged, but compressed, glands. The moment it reaches the decidua compacta, the decidual artery once again increases its girth, to follow an equally complicated course in a restricted part of the decidua compacta. This winding course brings the artery to a position near the axis of the decidua, deep to the placenta. The coils disappear, and in a short, straight course the artery reaches the placenta. This short, straight segment is greatly narrowed. However, as soon as the artery enters the developing placenta it becomes continuous with the widely distended intervillous spaces.

Certain features concerning the nature of the circulation during the first part of pregnancy require further elaboration. In the first place, the short segment of the decidual artery, as it lies in the muscularis, remains extremely delicate. In fact, so delicate in this short segment, that its position and course can be traced in serial sections only under high power of the microscope. Even then, on several occasions, the precise origin of this artery could not be ascertained by this technique. No differences could be detected between this segment and the other arteries of similar size in the myometrium. It is a remarkable phenomenon that this tiny branch should enlarge immediately on entering the decidua.

In the second place, the segment of the decidual artery, lying in the decidua spongiosa, can readily be distinguished from that lying in the decidua compacta. The former is to be found in the thin strands of the decidua lying between the crevices of the much flattened, middle segments of the glands (fig. 12). Although the artery in the decidua spongiosa continues to increase slowly in diameter, it is only when the somites of the embryo appear that the lumen of the artery in the decidua spongiosa has attained a size similar to that of the vessel located in the decidua compacta. This increase in diameter leads to a slight simplification of the coils. It might be added that the decidual artery in the decidua spongiosa displays regions where the coiling is very intricate, and these coiled parts are connected by relatively straight and short segments. By contrast the artery in the decidua compacta is uniformly coiled (fig. 67).

In their distribution the decidual arteries are sharply restricted to the decidua compacta and decidua spongiosa. In the originally lateral walls of the uterus, and thus also in the decidua pseudocapsularis, the blood-vessels may be slightly increased in size (fig. 15), but they are derived from arteries other than the decidual arteries.

On first impression it might be thought that the devious course, followed by the artery through the decidua spongiosa, is a consequence of the distortion of the middle segments of the uterine glands. However, on close scrutiny, it is at once apparent that the decidua is much thicker around the artery than elsewhere in the decidua spongiosa (fig. 67). In these thickened parts of the decidua spongiosa the artery coils upon itself in three planes in an intricate fashion. From fig. 67, it is evident that the decidual artery is very much longer than the relatively short segments of the decidua in which the artery is embedded. It is quite clear, therefore, that the complicated course of the artery through the decidua spongiosa, as well as through the decidua compacta, is not conditional on the form of the glands.

In the third place, it is noteworthy that a cap-shaped area of the decidua compacta, surrounding the placenta, remains *a*-vascular (fig. 35). It is traversed only by the thin, straight, terminal segments of the decidual arteries. This contrasts significantly with the extreme vascularity in the deeper regions of the decidua compacta (fig. 12).

Careful examination revealed the important fact that the decidual artery, throughout its entire course, remains as a continuous channel which does not give off subsidiary branches to supply specifically any part of the decidua. Occasionally the artery may bifurcate, and each part continues to follow a similar devious course to end eventually in the intervillous space of the placenta.

Perhaps the most phenomenal characteristic of the decidual artery is the extremely devious course pursued by this vessel from the moment it

enters the decidua spongiosa until it reaches the placenta. This cannot, by any means, be appreciated from the examination of a single section. Unless a three-dimensional reconstruction be made, no clear picture of the circuitous course can be gained. Even the two-dimensional projection, shown in fig. 69, provides only a glimpse of the complex behaviour of this vessel in a uterus associated with an embryo with approximately 35 somites. (Unfortunately the embryo was slightly damaged and the precise number of somites could not be enumerated accurately.) It should be added that at this stage of development the artery has already been almost completely remodelled in the decidua compacta and, therefore, the total length of the artery is greatly shortened; all the coils shown in fig. 69 are confined to that part of the artery lying in the decidua spongiosa. In earlier stages of development there is evidence which more than suggests that the coiled artery in the decidua compacta is even longer than that in the decidua spongiosa.

Despite the shortening of the coiled artery, which has already occurred, its length as projected in a tangential plane, shown in fig. 69, is not less than 7 cm. A fair estimate of the true length of the artery, coiling in space, would be 4 π times its projected length. This means that the total length of this decidual artery would be approximately 9 cm. The surviving segment in the decidua compacta measures 1·5 mm., so practically the total length of 90 mm. is to be found within the confines of the decidua spongiosa.

It should be added that the decidua spongiosa is restricted to a small part of the uterine swelling, the diameter of which at this stage is 10 and 6 mm. (*cf.* fig. 18). This means that the arterial length of 90 mm. is 10 to 15 times the total diameter of the uterine bulge. Moreover, when it is appreciated that there are usually three and occasionally four such arteries converging on the placenta, then it follows that these coilings of the uterine arteries unquestionably have a profound effect on the mechanism of the blood-flow through the placenta during the first half of pregnancy.

Thus far the course of a single decidual artery from its point of origin to its termination in the placenta has been described. However, as a rule, three decidual arteries supply the placenta in each uterine horn. Occasionally these arteries may be reduced to two, or sometimes there may be as many as four. Irrespective of the number, each decidual artery has its own individual origin at a different point along the circumference of the uterine bulge, and thereafter pursues its devious course through a circumscribed segment or a field of the decidua spongiosa and compacta. This is particularly well illustrated in a horizontal section of the uterine bulge (fig. 68). The uterine cavity in this section is occupied by the basal portion

of the placenta. The plane of section of fig. 68 is such that it nearly excludes the decidua compacta, as is evident from a comparison of this figure and fig. 14. As a consequence only the coils located in the decidua spongiosa are depicted. In fig. 68 the three arterial fields in the decidua spongiosa can readily be identified. These fields are separated from each other by *a*-vascular segments of the decidua spongiosa. This field disposition of the decidual arteries can also be appreciated from cross-sections of the uterus (figs. 15, 17).

Having traversed the decidua spongiosa and the decidua compacta, the three arteries converge to a very restricted area in the centre of the placenta. These vessels approximate so closely to each other near their termination, that in a single section two decidual arteries were seen to reach the embryo-chamber, while the termination of the third was only a few sections removed.

Whereas there are, as a rule, three decidual arteries, the decidual vein always remains single. The vein swells at the same time as the coiled arteries, and is then invariably found lying at the mesometrial pole of the uterus in the decidua spongiosa immediately underneath the muscularis. This vein, although swollen, has the characteristics of an ordinary vein. It receives tributaries from all parts of the decidua, and also a variable number of branches coming from the placenta. The placental branches are rather straight, but the branches coming from the decidua follow a more tortuous course. When all these tributaries have united into a single vein at the mesometrial pole, this vein continues its course in the decidua spongiosa for a considerable distance, until it reaches the line of attachment of the mesometrium to the uterine swelling; here it suddenly enters the muscularis and proceeds into the mesometrium.

The Terminal Portions of the Decidual Vessels and the Construction of the Placental Circulation.—In a previous section the vascular phenomena, encountered during the successive stages in the genesis of the placenta, have been already described. Now it remains to examine the fate of the decidual arteries, as they spend themselves in the elaboration of the placental circulation.

As already mentioned, when the embryo is about to erode the chamber wall (fig. 31), the decidual arteries have converged towards the chamber to form a subchamber capillary anastomosis. In this process two of the decidual arteries, as a rule, lie nearer towards one another than do the two of these to the third. When the cytotrophoblast enters the superficial part of the decidua compacta as a cone-shaped structure and, at the same time, erodes the distended capillaries, it would appear that the two contiguous vessels form, by the erosion of their separating walls, a single terminal channel, whereas the third artery, being a little removed, maintains its own

separate communication with the intervillous spaces. At this early stage the opening up of the subchamber capillary anastomosis implies the simultaneous opening up of the venous portion of the capillary bed. When the blood occupies the large spaces between the primitive chorionic villi, it is impossible, in section, to discriminate between the venous and the arterial lacunae of the young placenta. The study of later developmental stages gives conclusive evidence that the venules leave the peripheral part of the lacunar system. By virtue of the fact that the arteries converge towards a restricted area in the centre, the arterial blood enters the placenta through the centrally situated lacunae.

At this stage, therefore, the primitive placental circulation may be summarised as follows. The arterial blood enters the placenta in a restricted area near the centre in the form of two sets of arterial capillaries. The one set is formed by the convergence, and early fusion, of the terminal portions of two decidual arteries (fig. 16), while the other has its origin from the terminal part of the third decidual artery. These two sets of arteries pour their blood into the wide intervillous spaces near the centre of the early placenta. The blood, after percolating towards the peripheral lacunae, leaves the placenta by a series of more laterally situated venules.

The further elaboration of the placental circulation is intimately dependent upon the structural changes in the developing placenta. It will be recalled that the very young placenta is cone-shaped (fig. 35). The central portion is the most deeply penetrating part, while the periphery of the placenta is in contact with the surface epithelium only. Even the central part is only superficially lodged in the decidua. At an early stage a temporary stabilisation is effected, and reticular fibres become interposed between the tips of the chorionic villi and the contiguous regions of the decidua. Once this temporary stabilisation has been achieved, further growth of the placenta occurs in the direction of the uterine cavity (figs. 36, 37). With this growth the pattern of the original lacunar system becomes increasingly more complex (fig. 36), especially in the peripheral part of the placenta. This is attained by the proliferation of the chorionic tissue and the arrangement of the newly formed cords of cells into a maze-like pattern. At the same time the central lacunae, containing the arterial blood, merely elongate and remain in the form of single, straight channels, conveying the blood directly towards the embryonic surface of the placenta (fig. 37).

In this way the maternal part of the placental circulation is established long before the allantois makes contact with the placenta (fig. 15). Even after the allantois brings the foetal blood-vessels to the placenta, the basic pattern of the circulation of the maternal blood through the placenta itself remains practically unchanged throughout the whole of pregnancy.

After the contact with the allantois the placental part of the foetal circulation is integrated with the maternal.

Hitherto the main changes in the decidual arteries were confined to those parts immediately related to the placenta. The basic pattern of the circulation through the placenta itself was elaborated. The three decidual arteries, for the most part, still pursue their lengthy and devious course from their site of origin until they terminate as the two central placental arteries. Henceforth the placental circulation proper remains relatively unaltered, whereas the decidual arteries undergo a fundamental reorganisation, which culminates in a spectacular shortening of their course.

The Alteration of the Course of the Decidual Arteries.—When the embryo is in the primitive streak stage, each decidual artery follows a most tortuous course, meandering through the decidua compacta and spongiosa, and its length, from where it leaves the muscularis to its junction with the placental artery, is several centimetres (fig. 14). After the destruction of the decidua it follows a straight course and is about 2 millimetres long (fig. 21).

This enormous change in the direction and length of the artery is accompanied by a transformation of its wall. While the wall of the artery is thus remoulded it remains intact, and at no time is there any spillage of blood into the decomposing decidual tissue. It is difficult to ascertain how exactly the shortening of the artery is effected. The mere swelling may result in a slight simplification of its course, yet when it is already enormously swollen (fig. 14) it still follows its tortuous course. As soon as the artery, or part thereof, is liberated from the surrounding tissue during the destruction of the decidua, a strong longitudinal contraction of its wall sets in, resulting in a local straightening of the course. The destruction of the decidual tissue starts near the attachment of the placenta, and proceeds from there towards the periphery. *Pari passu* with this destruction the decidual artery is shortened and straightened out. In the 22-somites stage (fig. 16) the greater part of the decidua compacta is decomposed, here the artery is straight; only a few coils are left in the peripheral area of the decidua compacta, whereas in the decidua spongiosa the artery still follows its tortuous course.

When in early pregnancy the decidual artery starts to swell and thus becomes conspicuous, it can be seen that its wall consists of a very much flattened layer of endothelium, supported by a delicate reticulum of thin fibres. In the much swollen artery, prior to the destruction of the decidua, the endothelium is still recognisable (fig. 65). Soon thereafter, however, the destruction of the endothelium is associated with a penetration of the giant cells into the lumen of the artery. Many of these cells arrange themselves to form a new, irregular wall to the artery (fig. 66), as has been described in a previous section (see p. 484). This lining of large decidual

cells narrows the arterial lumen considerably. Thus at this critical time, when the artery is about to change from a long, tortuous to a short, straight channel, a constriction of the arterial lumen is interposed between the wide central placental artery on the one hand, and the distended tortuous artery on the other. With the continued destruction of the decidua compacta and spongiosa, this constriction shifts upwards along the artery. It can be seen in the peripheral part of the decidua compacta in fig. 16 at the right side; in fig. 19 it has reached the top of the decidua spongiosa. Finally, when the decidua spongiosa is also completely destroyed, or rather just before that time, the constriction will reach the place where the decidual artery enters the decidua from the muscularis. The whole decidual artery has then changed into a short and straight vessel. When exactly this change takes place could not be ascertained. At the time the embryo is 12·5 mm. long, a good deal of the decidua spongiosa, with the coiled artery in it, is still present, whereas the artery is straight when the embryo is 18 mm. long.

At this same time another noteworthy change in the decidual artery occurs that is probably of fundamental influence for the placental circulation. It has been mentioned that the decidual artery arises as a tiny side-branch of a myometrial artery. This branch, as far as it runs in the myometrium, remains extremely narrow, no matter how much the artery in the decidua is swollen. To follow the tortuous course of a decidual artery in a uterus, as figured in fig. 14 or 19, is only a matter of patience, but it is difficult to trace the connection with the myometrial artery. As long as anything is left of the decidua spongiosa, the connecting segment remains narrow, but when the whole decidual artery has been changed into a short and straight vessel, this vessel is continuous with an equally wide myometrial artery without any trace of a constriction (fig. 21).

The shortening of the decidual artery is accompanied by another change in the composition of its wall. Prior to the destruction of the decidua, the arterial wall is composed of large decidual cells. Thereafter these cells are also destroyed, and the wall now consists of a dense reticulum of coarse fibres, traversing the coagulated, necrotic debris (figs. 20, 21). This reticulum around the arteries is continuous with the anchoring layer of the placenta. Gradually it becomes attenuated as it extends along the main placental arteries. In the layer of columns it is very thin, and has almost disappeared from the radiating arterial branches (fig. 21).

Apart from the fibrous elements of the arterial wall, two types of cells may be recognised, enmeshed in the fibres. The first is a small cell with a very hyperchromatic nucleus, which could easily be mistaken for endothelium. This cell is derived from a small decidual cell, and is scattered irregularly in the arterial wall. The more numerous cell type occurs in small clusters; these cells are remnants of the second invasion of the

trophoblast into the decidua. The cells of this type are chiefly distributed between the fibrous wall and the surrounding necrotic debris.

The artery in the muscularis and in the mesometrium always retains its endothelial lining. As previously described (van der Horst and Gillman, 1946 *b*), the earliest reaction in the tunica externa is indicated by the formation of a definite cellular sheath in the media in the stage when the embryo has a primary amniotic cavity. This becomes more accentuated in the primitive streak stage, and the differentiation into the decidual cells is foreshadowed when the embryo has developed 13 somites. Only after the destruction of the decidua compacta and spongiosa is almost achieved, does the decidual reaction in the wall of the mesometrial artery reach its climax. The decidual cells around the myometrial artery also disappear gradually, and at parturition decidual cells are to be found only in the wall of the mesometrial artery.

As far as the vein is concerned, it is noteworthy that large giant cells do not form around and in the walls of the veins as described for the arteries. Although many of the tributaries are destroyed simultaneously with the decidua, the remoulding of the vessel is not so spectacular as in the case of the artery. Once the decidua is destroyed, structurally the wall of the vein is similar to that of the arteries, and in a section the character of a vessel, artery or vein, can be ascertained only by following its course through the placenta.

The Stabilised Placental Circulation.—With the total destruction of the decidua compacta and spongiosa, and the associated modifications in the walls of the arteries and veins, the placental circulation now becomes stabilised until the end of pregnancy. The remarkable metamorphosis of all the tissues comprising the decidua, including the arteries and veins, which permits the emergence of the stabilised placental circulation, can be readily appreciated from a comparison of figs. 67 and 71. Whereas in fig. 67 the decidual arteries and veins follow a most complicated course through both the decidua compacta and spongiosa, once the subplacental tissues are destroyed, both the arteries and vein acquire a direct pathway to and from the placenta (fig. 71).

The circulation which persists until the end of pregnancy may now be reviewed. The mesometrium, enclosing the main artery and vein, is attached to the uterus at a position corresponding almost to the centre of the placenta. Some distance removed from the mesometrial reflection on to the uterus, the artery and vein have a parallel course, but their walls are distinctly separated from one another. Close to the mesometrial attachment the artery and vein come into intimate contact. At first the artery only slightly indents the wall of the vein. This indentation becomes rapidly more pronounced, until eventually the artery is suspended within

the lumen of the vein by a delicate ligament only. The surface of the latter, exposed to the blood lying in the vein, is covered by a layer of endothelium. In some parts along its course this arterial ligament disappears completely, with the result that a greater or shorter segment of the artery lies completely free in the lumen of the vein, but covered by an endothelial lining. The artery, therefore, has both an outer and an inner layer of endothelium (fig. 70).

This intravenous artery follows a winding course through the lumen of the relatively straight and very wide vein, until a little distance before it enters the myometrium. Here the artery emerges from the vein to follow an independent course. In the myometrium the artery divides into branches which are distributed exclusively to the myometrium and into two or three wide placental arteries. The latter run for a little distance in the muscularis, where they diverge from each other. Some distance removed from the centre of the placenta they leave the muscularis to become the decidual arteries. These three decidual arteries curve back sharply on their course, converging towards the centre of the placenta to form the placental arteries.

The original length of the decidual artery, from its point of origin to its entrance into the decidua compacta, was 90 mm. (fig. 69). To this must be added the length of the artery in the decidua compacta, which is at least as great as that in the decidua spongiosa. The final length is about 2 mm. This means that, when the placental circulation is stabilised, the decidual artery has been shortened to approximately one-hundredth of its original length. A direct channel is, therefore, established between the mesometrial and placental arteries.

As previously indicated, the decidual arteries, as they lie in the debris left after the decomposition of the decidua, lose their endothelium, and their walls then consist of a thick layer of compact fibres between which the remnants of some trophoblastic cells may be identified. The fibrous wall of these arteries, as well as of the vein, provide the only attachment of the placenta and, therefore, of the foetus, to the uterine wall.

Having attained a position immediately deep to the placenta, two arteries, as a rule, unite to form one placental artery. The third decidual artery continues independently as the other placental artery. These two placental arteries follow a straight course through the centre of the placenta, without distributing any side branches and without altering the calibre of their lumen. Having traversed the placenta, the two arteries reach the free surface of the placenta, where they come into close contact with the umbilical vessels. From the centre of the free placental surface the placental arteries branch into a variable number of radiating arteries distributed over the surface of the placenta. Each of these radial arteries

in turn sends off small radicals, which may again divide and then enter the layer of columns. The walls of these columnar channels, containing arterial blood, consist only of a much flattened, syncytial layer, derived from the cytotrophoblast. Having left the columnar layer, the maternal blood now passes into devious channels constituting the spongy layer of the placenta. These channels pursue a winding course through the spongy layer, but their calibre does not materially alter until the deepest part of the placenta is reached. Here they fuse into a number of larger channels, which may be regarded as the beginnings of the placental vein. All these venules eventually unite to form a single vein. This vessel structurally is very similar to the decidual arteries, and pursues a straight course to the mesometrium, where it comes in close contact with the artery. Soon after entering the mesometrium the vein dilates greatly to accommodate the twisted mesometrial artery. The extra-uterine length of the vein is 12 mm., and it pursues a straight course to its termination in the inferior vena cava.

In *Elephantulus*, as in other mammals, two allantoic arteries and one vein are responsible for the placental part of the foetal circulation. The two arteries reach the centre of the placenta before they divide into numerous radiating branches, which intertwine with the corresponding radiating branches of the maternal placental artery. From these radiating and arborising vessels small branches arise that penetrate into the placenta and traverse the columnar layer in a more or less diagonal direction. This course makes these diagonal arteries a conspicuous feature in a cross-section of the placenta, and in nearly every section a few of them could be seen. At the junction of the columnar and spongy layers of the placenta, the diagonal arteries are continued into a number of horizontal branches, from which arise the numerous capillaries that again enter the columnar layer. These capillaries pursue a straight course through the columnar layer, parallel to the narrow channels that convey the maternal blood. The foetal blood here is separated from the maternal blood by a delicate layer of foetal endothelium and by a single layer of flattened, trophoblastic syncytium. On the embryonic surface of the placenta, the foetal blood again is collected from the straight capillaries into radiating veins, and these in turn combine in the centre of the placenta to form the single umbilical vein.

The presence of the conspicuous diagonal arteries made it relatively easy to establish the direction of the embryonic blood-flow in the columnar layer of the placenta without any doubt. It is evident that here the foetal and the maternal blood flow in opposite directions in the narrow, straight capillaries or channels that compose the columnar layer. It is equally evident that no foetal blood enters the spongy part, whereas the maternal blood, on leaving the columnar layer, continues its course into the spongy part of the placenta. This part of the placenta, therefore, contains only

maternal blood that, on the whole, flows from the embryonic side towards the attached base of the placenta. The foetus establishes close contact with the maternal blood only in a narrow zone of the placenta, whereas the greater part of the placenta is never vascularised by the allantoic vessels. The complete placental circulation is initiated when the embryo has 18 somites, is stabilised when the embryo is about 18 mm. in length, and thereafter persists relatively unchanged until the end of gestation, when the foetus is nearly 40 mm. long.

Discussion.

It is not the intention to discuss every single fact or observation mentioned in the descriptive part. On the other hand, there are several morphological features of the embryological development of *Elephantulus* that can be looked upon from different angles, and they may shed light on more than one question of mammalian development. Such facts may be mentioned repeatedly in the following pages.

The Localisation and Orientation of the Implantation Site.

With localisation is meant the place of the implantation site in respect to the longitudinal axis of the uterus, and with orientation the place with regard to the mesometrial attachment.

Mossman (1937) has shown, and laid down in a comprehensive table, that the embryos of many placental mammals implant themselves in the uterine wall in a specific way. The implantation site is orientated in respect to the mesometrial attachment in a manner characteristic for each species, it may be mesometrial, antimesometrial or lateral. Directly related to the orientation of the implantation site is its localisation over the length of the uterus or uterine horns, and in this respect some variat on exists amongst the placental mammals. A few examples will be give first by way of introduction.

In some mammals, as in the pig, there appears to be neither localisation nor orientation. All parts of the uterus equally favour the continued development of the embryo.

In monkeys and man the embryo can apparently also implant itself anywhere in the uterus, although implantation in or near the fundus is the rule. In the macaque, statistics have shown that implantation occurs more frequently in the dorsal wall of the fundus than elsewhere.

Again in other mammals, as in the rat, although the embryos can be dispersed along the whole length of the uterine horns, nevertheless the implantation site is orientated in a specific way in relation to the mesometrial reflexion. Such a constant orientation implies that one area of the

uterus has properties different from those of the rest of the uterus; a specific localisation may be attributed to the same cause. In the case of the rat this specialised area extends over the whole length of the uterine horn. While rat embryos can implant themselves along the antimesometrial side of the uterus only, in Centetes the lateral implantation allows an alternative in so far as the embryo may affix itself to the right, or to the left, wall of the uterus. With this limitation, in both these animals there is a definite orientation but no localisation.

In *Elephantulus* the implantation site is not only orientated, but it is also restricted to one particular spot along the length of the uterus. Both localisation and orientation, therefore, are determined.

In the same table, mentioned above, Mossman laid down the orientation of the embryonic node in respect to the mesometrium in the various mammals. This, however, is quite a different problem (van der Horst, 1949 *b*); the position of the embryonic node is not directly related to the constitution of the uterus.

In general, it can be added that the position of the embryo, either in the main uterine lumen or in a restricted part thereof, or even in the case of interstitial implantation, bears no direct relation either to the localisation or the orientation.

In the pig, with its diffuse, epithelio-chorial placenta, when the embryo has reached a certain stage of development, it can stimulate the entire length and breadth of the endometrium to react in the appropriate way. This reaction is restricted to the region in which the embryo happens to find itself. The endometrial reaction, therefore, is neither localised nor orientated, and its position is entirely a function of the embryo itself.

On the other hand, in the Lemuroidea, also with a diffuse placenta, only a certain part of the uterus seems to be reactive. At least in Galago the twin embryos are always located near the lower end of the uterine horns. It is possible, of course, that the rate of growth of the early embryo is such that it has already reached the lower end of the uterine horn before it is able to stimulate the uterine wall sufficiently. It is more likely, however, that only this lower end of the horn is reactive, in which case there should be localisation, but no orientation, in Galago.

It is to be expected that no orientation occurs in all those mammals which have a zonary placenta, like the Carnivora and Procavia. Also localisation seems to be absent in these cases. In *Procavia*, the one or two embryos in each uterine horn can be found anywhere over the length of the uterus (Sturgess, 1948). Here again it appears as if the embryo determines where it will induce the uterine reaction, necessary for its continued development.

On the other hand, there are indications that in Orycteropus, which

also has a zonary placenta, both localisation and orientation occur. Only a single case of early pregnancy of this animal has been available for study (van der Horst, 1949 *c*). The allantoid placenta was confined to the mesometrial half of the uterus; this is the only and dubious indication of orientation. It is known that *Orycteropus* bears a single embryo at a time; also in this case there was only one embryo in one of the uterine horns. Yet both ovaries had liberated eggs, as shown by the presence of five corpora lutea. The explanation of this may be in the presence of a strict localisation.

The fact that both in man and the macaque the embryo can, on occasion, implant itself in any part of the endometrium, and even over the cervix, as happens in placenta praevia, would suggest that, provided the uterus is adequately sensitised, implantation is primarily dependent upon the embryo itself. In man, the decisive rôle of the embryo in determining the implantation site is particularly well illustrated in ectopic pregnancies. However, implantation occurs much more frequently in the fundus both in the human female and in the macaque. In both the fertilised ovum is very slowly transported down the tube (see p. 514). Therefore, the embryo may have developed sufficiently to permit implantation by the time it enters the uterus. Moreover, a series of irregular, transverse, endometrial folds in the fundus may impede a speedy descent to the lower part of the fundus. A rapid transportation of the embryo, possibly in conjunction with a relative underdevelopment of these mucosal folds, may occasionally facilitate implantation in the body, or even in the lower region, of the uterus. With the slow transportation it is more likely that the embryo, at the critical stage of its development, will usually find itself in the uterine fundus, but no matter where it is at that moment of time, the embryo will attach itself anywhere to the maternal tissue, and there excite the appropriate reactions. On the whole, therefore, in man the embryo determines the site of implantation.

A different state of affairs exists in those mammals in which the implantation site is definitely orientated. Here the embryo can no longer implant itself *ad libitum* anywhere in or outside the uterus, but it is restricted to a circumscribed area of the endometrium. In some mammals this area extends over the whole length of the uterus. This seems to be the case in all species that usually produce a rather large litter. The embryos then can implant themselves anywhere over the whole length of this specialised strip of endometrium. However, some mechanism needs to be elaborated to facilitate an adequate spacing of the embryos in the uterus. As soon as an embryo arrives at a particular spot, a local interaction between the embryo and the endometrium sets in, making the immediate neighbourhood refractory to implantation of other embryos.

It may be presumed that some morphological difference, be it only at the chemical level, exists between this strip and the rest of the uterus. This is shown by the neat experiments of Alden (1945). He rotated 180 degrees part of the uterine horn in the rat, leaving the arteries intact. When these animals were mated, the eggs implanted themselves in the antimesometrial wall of the uterus in both reversed and unreversed segments. Gravity, or some other outside influence, inducing the embryos to implant at a particular side of the uterus, is therefore excluded; it is the structure of the uterus itself that determines the side at which implantation will take place.

In the primipara this reactive strip extends, without interruption, over the whole length of the uterus. In subsequent pregnancies, however, certain parts of the uterus do not favour implantation as much as do others.

Droogleever Fortuyn (1929) found that in the striped hamster the old implantation sites are apparently no longer able to receive embryos. Similarly Strauss (1944) demonstrated that in Ericulus the embryos implant themselves between the sites occupied during a previous pregnancy. But even so the embryos still have a wide choice. Nevertheless, in all these mammals the implantation site is no longer determined exclusively by the embryo alone, but also by the structure of the uterus. There is a strict orientation but no localisation of the implantation site.

Still more restricted than in the rat is the embryo of the golden moles in the choice of its implantation site (van der Horst, 1948). Although the embryo can implant itself, *ad libitum*, either in the right or the left lateral wall of the uterus, implantation can only occur in the lateral walls. Moreover, it seems that nidation is possible to the twin embryos only in a restricted part along the length of the uterine horn. Therefore in the golden moles, although some freedom is left, both localisation and orientation are restricted.

In *Elephantulus* there is no doubt at all that the place of implantation is predetermined entirely by the structure of the uterus. Nidation of a single embryo is possible only at the mesometrial side in a very restricted area near the posterior end of each uterine horn. In all the material of hundreds of pregnant uteri, implantation was never observed other than at this particular spot. Both orientation and localisation are carried out to the extreme in *Elephantulus*.

This is borne out by two other observations. Firstly, menstruation only occurs from a very circumscribed part of the endometrium, located at the same place where implantation takes place, *i.e.* at the mesometrial side, and near the caudal end, of the uterine horn (van der Horst and Gillman, 1941 *b*). At this place a smaller or larger mass of endometrial tissue grows out, and projects like a polyp into the uterine lumen. This polyp subsequently undergoes necrosis and is thrown off, but the resulting wound is

very small. The striking picture presented by a uterine horn with a large polyp serves to emphasise the extremely small part of the uterus involved in the menstrual process.

In the second place, in two cases in the collection of sectioned uteri, two embryos had apparently arrived simultaneously, or at least immediately after one another, at the implantation site and there formed an embryo-chamber (van der Horst, 1949 *a*). However, there was insufficient space in the chamber to accommodate both embryos, so one continued to develop on top of the other. These two spontaneous experiments demonstrate forcibly that no other region of the uterus, even close to the area of predilection, favours implantation. The possible cause of this strict limitation will be discussed later on (p. 549). Suffice it to state at this junction that both localisation and orientation are absolutely determined in *Elephantulus*.

The Form of the Conceptus in Relation to the Size of the Embryo.

The mammalian embryo arrives at the implantation site at an early stage of its development. With the growth of the embryo and its membranes, together with the associated reaction of the uterus, the conceptus gradually acquires a characteristic size and form. Even though the embryo increases in size during pregnancy, the form of the conceptus in some mammals, e.g. *Procavia*, may remain more or less constant. On the other hand, in *Elephantulus* a succession of different forms of the conceptus occurs during the course of pregnancy. Irrespective of whether or not there is a change in form, the pattern is remarkably characteristic for each species of animal.

As Mossman (1937) has shown, the position of implantation may conveniently be orientated in respect of the mesometrial attachment. Thus he classified the position of implantation in the different mammals as mesometrial, lateral, antimesometrial and circumferential. This orientation, like the form, is characteristic for each species of animal.

Despite this constancy in the shape of the conceptus, and also in the orientation of the embryo, no efficient correlation can be established between these two phenomena. While the circumferential implantation is almost invariably associated with a radial symmetrical swelling of the uterus, such a type of swelling is no indication of the location of the placenta. In the hedgehog, for example, the embryo implants itself antimesometrially, yet the shape of the early conceptus is spherical. On the other hand, an embryo may implant itself in one or the other pole of the uterus and, during its growth, produce a one-sided swelling of the uterus. This may even be intensified with the progress of pregnancy as in the Soricidae (Hubrecht, 1893), or, as in *Elephantulus*, the form may first be hemispherical, then spherical, and finally cylindrical.

Reynolds (1946) showed that, in the rabbit, the accommodation of the conceptus by the uterus follows a pattern which may be divided into three distinct phases. These are (1) a period of uterine preparation, (2) a period of uterine enlargement, and (3) a period of uterine stretching. These same periods can clearly be recognised in *Elephantulus*, with this addition, that the third period can be subdivided into two phases.

The first period is characterised by mitotic proliferation of uterine tissues, with no appreciable increase in the size of the uterus, but with an increase in the number of component parts of the uterus, which are available for subsequent hypertrophy in the next phase. This period starts in *Elephantulus* before ovulation, and it ends when the four-celled blastula reaches the implantation site. This is discussed in the section on the Pre-implantation Reactions (p. 514).

The second period commences soon after implantation; during this period the weight of the uterus increases considerably by a hypertrophy of the tissue elements. It is a period of active growth of the uterus. In some, if not in most of the mammals, this growth extends over the whole circumference of the uterus at the place where the embryo is located. It is so in the rabbit, in *Procavia*, *Erinaceus*, *Oryeteropus* and many others, resulting in a more or less spherical swelling of the uterus. In *Elephantulus* originally only a very small segment is involved, but here the growth is most vigorous (fig. 1). Only in this segment does the decidual reaction, accompanied by a great enlargement of the individual cells, take place, and the glands here swell to an enormous size. But the uterine wall does not become thinner, except for the myometrium. The reaction to the presence of the embryo is an active growth of the wall. This growth is confined to a small segment at the mesometrial pole of the uterus, and by its growth this segment finally occupies at least half of the circumference of the uterus. The antimesometrial part of the uterine wall remains totally unaffected. As the mesometrial attachment is not located exactly at the mesometrial pole, but slightly to the dorsal side of it, the result of this one-sided swelling is that the place of attachment seems to shift over the surface of the uterus to the lateral wall.

During the third period, recognised by Reynolds, the rate of growth of the uterus decreases, and the uterine wall is stretched more passively. In the rabbit, this stretching is accompanied by a change in form of the conceptus from spherical to cylindrical. The diameter no longer increases; only an enlargement in longitudinal direction takes place. This is different in *Elephantulus*. Here the growth of the mesometrial side of the uterus suddenly comes to a complete stop; this side may even become smaller by shrinkage. Only the, hitherto inactive, antimesometrial wall of the uterus is stretched by the growing embryo. The result is that the conceptus

changes from a hemispherical to a spherical form. Further, the mesometrial attachment seems to return to its original place near the mesometrial pole of the uterus.

The change from a hemispherical to a spherical shape of the conceptus is initiated in *Elephantulus* when the embryo is 5 to 6 mm. long, and the spherical form is retained until the embryo has reached a length of about 20 mm. From then onwards the transverse diameter of the swelling remains the same, and further stretching of the uterine wall occurs in the longitudinal direction only. This is different from Reynolds' observations in the rabbit, although this change in the direction of stretching does not seem to be of the same importance as the conversion from the hemispherical to the spherical form. The latter begins when the embryo is about 6 mm. long, and this change is related to some important events in the development of the embryo (fig. 19). The decidua pseudocapsularis is, of course, directly affected, and disappears as a separation between the bursa embryonica and the main uterine lumen. The destruction of the decidua sets in long before and will continue for a considerable time, so this destruction is not related to the change in form. But noteworthy is that the decidual reaction by this time has involved the whole decidua spongiosa, and a further extension in the uterus of this reaction is impossible, except along the myometrial and mesometrial arteries, where it bears another character. Further, the allantois has enveloped the whole yolk-sac, which means the end of the yolk-sac phase of nutrition. Also, when the embryo is 6 mm. long, the vestigial, secondary placenta makes its appearance. All these events are related to each other.

The change from the hemispherical to the spherical form of the uterus in *Elephantulus* is an external manifestation of a critical moment in the development of the embryo.

Embryo-chamber, Decidua Capsularis and Decidua Pseudocapsularis.

It is a common sight, in *Elephantulus*, to find a number of healthy, four-celled embryos dispersed over the length of the Fallopian tube and the upper part of the uterine horn. At the time of ovulation, and during the period of descent of the embryos, the uterine lumen is wide open, but as soon as the first embryo has reached the implantation site, a contraction of the uterine wall takes place, and the lumen over the whole length, above the implantation site, is closed (see p. 516). A further descent of all other embryos is thus prevented. The contraction of the uterus may be so vigorous that the early embryos are crushed. Sometimes the contraction is not so strong; this, in particular, occurs when the animal was fertilised immediately after the end of a previous pregnancy. In such a case the

trapped embryos may survive for some time, although their further development is not normal (van der Horst and Gillman, 1944). A regular spherical cavity, with one-half of the sphere in each of the two opposing parts of the uterine wall, is then formed, in which cavity the trapped embryo fits. Strauss (1943) described similar spherical cavities, containing early embryos, in *Ericulus*; Sansom (1937) found them in *Crocidura*; and Hill's figure of *Loris* (1932) is also very similar. In these animals the formation of these spherical cavities precedes implantation of the embryo at that place. In *Elephantulus*, however, no further reaction follows, neither in the embryo nor in the endometrium. The epithelium remains perfectly healthy, and the adjoining stroma does not show any alteration. Soon the embryo in such a cavity disintegrates, and the uterine walls flatten out. As the one successful embryo also becomes lodged in a similar cavity, false embryo-chamber seems to be an appropriate name for the temporary spherical cavity. False embryo-chambers may be found over the whole length of the uterine horn. Their occurrence is remarkable, because of the difference in reactivity shown at the implantation site where the real embryo-chamber is formed, compared with anywhere else in the uterus.

When the one successful embryo arrives at the implantation site, situated at the mesometrial end of the slit-like uterine lumen, the endometrium and the epithelium locally withdraw in front of the embryo. In this way a thimble-shaped niche is formed in which the embryo is lodged, and in which it closely fits, as long as it is in the blastula stage. Embryo-chamber may be the best name for this niche. Most authors have used the term egg-chamber for the widening of the uterine lumen in which the mammalian embryo is lodged. However, in *Elephantulus* embryo-chamber seems to be more appropriate, and the name egg-chamber is better reserved for the widening of the Fallopian tube, in which the eggs sojourn for a while and where they are fertilised.

No explanation can be given about the actual cause, nor about the method, of the formation of the embryo-chamber. No trace of it can be seen when the 4-celled embryo arrives at the implantation site (fig. 4); it is in the process of formation when the embryo consists of 8 cells (fig. 5), and it is well established at the 32-celled stage (figs. 6, 7, 8). During its formation the chamber is surrounded by a loose, oedematous tissue (fig. 5); when it is fully formed this tissue is much denser (figs. 7, 8); this density is the beginning of a decidual reaction in the endometrium. Moreover, the niche is strictly limited to the place where the embryo is situated; this, in particular, is shown in longitudinal sections (fig. 8). The false embryo-chambers could be explained as being imprints of the spherical embryos; in the case of the real embryo-chamber such an explanation is untenable. It can only be said that the formation of the embryo-chamber

is caused directly by the presence of the early embryo, but that it is formed by an active withdrawal, or recoiling, of the uterine tissue in front of the embryo. The mechanism, however, remains a mystery.

A similar embryo-chamber has not been observed in any other mammal. In *Erinaceus*, according to Hubrecht (1898 *a*), the two folds of the endometrium, and the slit between them in which the embryo will settle, are formed before the egg arrives, and also in *Gymnura*, Hubrecht mentions a considerable proliferation of maternal tissue, at the implantation site, when the blastocyst is still in the oviduct. So in *Erinaceus*, the slit is formed between two outgrowths into the uterine lumen, and this is not caused by the presence of the embryo at the actual spot. This slit in *Erinaceus* and in *Gymnura* cannot be compared with the embryo-chamber of *Elephantulus*. In *Cavia* the embryo eats a clear-cut round hole through the uterine epithelium, as described by Sansom and Hill (1931), and in *Macacus* it fixes itself to a flat layer of uterine epithelium and, directly upon arrival, sends its primitive villi into it (Heuser and Streeter, 1941). In neither case is there anything comparable to the embryo-chamber of *Elephantulus*.

Only in man do we encounter a process of implantation that is reminiscent of the formation of the embryo-chamber in *Elephantulus*, although at first sight it looks quite different. The human embryo arrives at the spot where it will implant when it is in the blastocyst stage, and it at once here destroys the uterine epithelium and adjoining stroma, so that it sinks into the substance of the uterine wall. It may be mentioned here that the figure of a human embryo sunk half-way in the uterine wall, given by Hertig and Rock (1945), has practically the same appearance as an embryo of *Elephantulus* in the same stage of development, except that in the latter the yolk-sac is slightly larger. The human embryo continues to penetrate deeper into the maternal tissue, until finally it is completely embedded, and the rim of the wound closes to form the decidua capsularis over the embryo. The embryo of *Elephantulus*, when it arrives at the implantation site, is too young and imperfect to destroy the uterine tissue; this tissue withdraws in front of it, and thus the embryo-chamber is formed. Only later, when the embryo is in the blastocyst stage, does it destroy the epithelium of the chamber and the adjoining stroma, and sends out its villi into the maternal tissue. The edge of the embryo-chamber of *Elephantulus* corresponds to the rim of the uterine wound in man. Often, it can be observed, this edge contracts, leaving a narrow opening between the embryo-chamber and the main uterine lumen (fig. 9). Before it can close completely, the yolk-sac grows out into the main uterine cavity, and this prevents the formation of a decidua capsularis (figs. 10, 11). Thus in *Elephantulus* there is only a temporary indication of a decidua capsularis.

I am in agreement with Hubrecht (1898 *a*) that the so-called decidua

reflexa of some rodents cannot be compared with that of man and the anthropoids. However, it is doubtful whether the decidua reflexa of *Erinaceus* and *Gymnura* is the same structure as found in man, and as indicated in *Elephantulus*, as Hubrecht maintains. In these animals the preformed slit closes behind the embryo by a fusion of the opposite walls, and only then does the embryo, now completely enclosed, start to erode the epithelium, and later to distend the fused lips to a thin membrane. Resink (1903) agrees with Hubrecht, and says that the origin and further development of the decidua capsularis of *Erinaceus*, and the fact that uterine glands open out both on the outer and inner surfaces of these coalescing folds, are so many points that demonstrate its homology with the decidua reflexa of man. Although a few glands may open into the embryo-chamber of *Elephantulus*, these glands have primarily nothing to do with the formation of a decidua reflexa.

Whether the structure, described by Wislocki (1940) in *Solenodon*, represents a last rest of a decidua reflexa, can be decided only when earlier stages of development of this animal become known. On the other hand, the decidua reflexa, described by Hamlett (1935) in the bat *Glossophaga soricina*, agrees in every respect with that of man, whereas in *Myotis lucifugus*, according to Wimsatt (1944), a decidua capsularis is absent, as the penetration of the embryo is incomplete.

As described by Hubrecht (1893) and by Brambell and Perry (1946), *Sorex* has an annular cushion formed by a thickening of the lateral wall of the conceptus. Underneath this cushion rifts appear, deep in the mucosa, which become confluent, and open into the uterine lumen at the mesometrial side of the cushion. In this way a decidua lateralis is formed, hanging down in mesometrial direction and surrounding the embryo like a curtain. Brambell and Perry are of the opinion that this decidua lateralis is homologous with the lateral parts of the decidua capsularis, as found in *Erinaceus*, so that *Sorex* would have an incomplete and transient decidua capsularis. However, the formation of the decidua lateralis of *Sorex* clearly shows that this structure is quite different from any part of the decidua capsularis.

On the other hand, I agree with Brambell and Perry that the diaphragma-like fold, which they found in *Sorex araneus*, is not a decidua capsularis. This fold is much better developed in *Crocidura*, in which animal it may even completely close for a short time (Sansom, 1937). It corresponds to the structure so evident in *Elephantulus*, which has been called decidua pseudocapsularis. When the embryo is in the primitive streak stage, and the umbilical vesicle has already reached considerable dimensions, the mucosa forms an annular swelling underneath the umbilical vesicle, and in this way the bursa embryonica is separated from the main uterine lumen.

In *Crocidura*, and especially in *Sorex araneus*, this fold is thin, although it is broad in the former; in *Elephantulus* it is a thick mass of mucosal tissue, containing swollen glands. But even so the decidua pseudocapsularis is only a transient structure, and the separation of the bursa embryonica from the main uterine cavity is never complete.

Also the fold described by Strauss (1943) in *Ericulus*, and considered by him to be an incomplete decidua capsularis, is evidently the same as the decidua pseudocapsularis of *Elephantulus*.

It is remarkable that in *Elephantulus* an attempt is twice made to separate the embryo from the main uterine cavity. First a vestigial decidua capsularis is formed, and later a decidua pseudocapsularis is interposed between the large bursa embryonica and the main uterine cavity.

The Trophoblast.

It has already been mentioned that the trophoblast, as such, is restricted in its occurrence to the monodelphic mammals only (van der Horst, 1945, 1949 *b*). The trophoblast is no other than the chorionic ectoderm differentiated and separated off from the rest of the embryo at a very early stage of development. In reptiles, birds and the lower mammals the chorion plays an important rôle in the metabolism of the embryo. In the Monodelphia, with eggs practically devoid of yolk, the nutrition of the embryo is dependent, from the beginning, on the food supplied by the surrounding uterus. Hence the first thing the embryo does is to form an organ for the absorption of that food.

Corresponding with the needs of intra-uterine life, the ectodermal layer of the chorion separates at a very early period of development from the rest of the embryo and its membranes in the monodelphic mammals, and is then known as trophoblast, the name given to it by Hubrecht. In *Elephantulus* the differentiation of the trophoblast is rather late, when the segmentation cavity is already present; the phylogenetic development of the trophoblast in this primitive mammal is still *in statu nascendi*. There are a few other mammals in which the differentiation of the trophoblast is not immediately so completely effected as is usually the case. In the bat, *Xantharpya amplexicaudata*, Kohlbrugge (1913) found that the entodermal cells are formed from the trophoblast as well as from the node, and, according to Sansom (1937), the entoderm of *Crocidura* at first has a mesenchymatous character before it assumes the form of a continuous layer; this fact points in the same direction. Heuser and Streeter (1941) also found evidence in the macaque that primitive entodermal cells are locally delaminated from the trophoblast. On the other hand, it is noteworthy that in *Tupaia*, supposed to be the nearest relative of the Macro-

scelididae, we meet with just the opposite; and the trophoblast is already separated from the inner cell-mass when the latter consists of one single cell only (Hubrecht, 1895).

In many Placentalia the trophoblast has still another important function, viz. that of fixing the early embryo to the uterine wall as a precursor to the formation of a more elaborate placenta. The rather late differentiation of the trophoblast in *Elephantulus* may be related to the presence of an embryo-chamber, in which the early embryo is securely lodged.

The trophoblast destroys the uterine epithelium and the adjoining stroma, so that its villi can penetrate into the maternal tissue. This penetration, at first, serves only for anchoring the embryo; in *Elephantulus*, at least, the embryo is surrounded by food, supplied by the uterine glands, and for a considerable time it does not need any other source of nutrition.

The histiolytic function of the trophoblast is altogether absent in mammals with an epithelio-chorial placenta; neither is it of great importance in those with a cotyledonous placenta. On the other hand, the histiolytic function of the trophoblast seems to be highly active, and also of long duration, in those mammals in which histiotrophe is the most important source of nourishment for the embryo, even if, as in the Carnivora, the walls of the maternal capillaries are not destroyed. But when the embryo gets its food mainly, or exclusively, by way of an exchange between the maternal and foetal blood, as in mammals with a haemo-chorial placenta, the histiolytic action of the trophoblast is of short duration and very local in extent.

In *Elephantulus*, the epithelium of the embryo-chamber degenerates and becomes necrotic soon after the nidation of the embryo, but this necrosis occurs only where the trophoblast is in direct contact with the uterine epithelium. There is a sharp and clear edge to the healthy uterine epithelium immediately the contact with the trophoblast is lost. That this direct contact is necessary has been observed in several animals. Vernhout (1894), for example, mentions that as soon as the trophoblast touches the uterine epithelium the latter is absorbed in *Talpa*, but where the trophoblast bulges inwards over the funnel-like openings of the glands, there the healthy epithelium has a sharp edge nearly touching the trophoblast; this also can be observed in *Orycteropus* (van der Horst, 1949 *c*). Sansom and Hill (1931) found that, in *Cavia*, a small clear-cut gap is formed in the uterine epithelium, just large enough for the passage of the embryo.

In *Elephantulus* a small part of the surface of the early embryo protrudes through the opening of the embryo-chamber into the main uterine cavity. This small part soon grows out to a voluminous yolk-sac, the trophoblastic wall of which is in direct contact with the uterine epithelium. Yet the latter does not show any sign of necrosis. It might be supposed that this small part of the embryonic surface has no histiolytic power at

all. Goetz (1938), for example, found that, in *Hemicentetes*, the histiolytic potential is restricted to a small part of the trophoblast only, and from Sansom and Hill's description it appears that a similar difference exists between the ectoplacental and parietal trophoblast in *Cavia*. However, no histological difference can be observed in the cells of the trophoblast in the early blastocyst stage of *Elephantulus*. Further, in the single embryo that was interstitially embedded, villi had grown out over the whole surface, and the maternal tissue was destroyed all round, in the same way as in *Erinaceus* or man. From this we may conclude that all cells of the *Elephantulus* blastula equally possess the histiolytic potential; only the cells, in contact with the chamber wall, can make use of it, and in all cells it is only of short duration. Also in *Cavia* (Sansom and Hill, 1931) the trophoblast normally exhibits no further evidence of destructive activity once the parietal trophoblast has produced a gap in the uterine epithelium, through which the blastocyst penetrates. When in *Elephantulus* the maternal epithelium of the embryo-chamber is absorbed and the trophoblast has penetrated slightly deeper, destroying a small area of the connective tissue and opening some maternal capillaries, further histiolytic activity of the trophoblast comes to an end also here, at least for some time.

We may therefore conclude that in some mammals, *Cavia* and *Hemicentetes*, the histiolytic action is restricted to a part of the trophoblast only, whereas in others, like *Elephantulus*, this action is of very short duration.

Hill (1932) remarks that, different from *Tarsius*, the syncytio-trophoblast of the Pithecoids is endowed with potent cytolytic properties, and he writes: "Viewing it from the standpoint of Professor Grosser, the most remarkable feature of the Lemuroid trophoblast is, it seems to me, the complete loss it has suffered of active invasive qualities it must have originally possessed. I suggest it is more likely that it had never acquired them." *Hemicentetes*, *Cavia* and *Elephantulus* give evidence that the cytolytic properties of the trophoblast can be very restricted in area and in time, from which it might be concluded that these properties can easily be lost altogether.

The Polar Differentiation of the Early Embryo.

Polarity of the embryo becomes evident at an early stage of development in the Marsupials. In *Dasyurus*, the fourth cleavage results in the differentiation of eight formative cells at the one side, from eight non-formative cells at the other, and henceforwards these two kinds of cells will occupy the two opposing halves of the embryonic vesicle (Hill, 1910). According to Hartman (1916), it is probable that such a polarity also exists in *Didelphys* at the same stage of development, although it is not reflected

morphologically; polar differentiation in this animal becomes evident only when there are about 40 cells. This differentiation into a formative and a non-formative half is reached when the spherical embryo is still enclosed in its zona pellucida, and when all sides are equally subjected to possible influences from its surroundings inside the uterus. The polar differentiation of the embryo is determined by the structure of the egg. This, of course, is even more evident in the reptiles, birds and monotremes.

In the placental mammals the non-formative half of the marsupial embryo does not exist any more. The whole mammalian morula corresponds to the formative half of the early marsupial embryo. A differentiation, with a polarity as its consequence, as found in the Marsupialia, therefore, cannot occur in the placental mammals. Even when the outer layer of cells of the morula has differentiated into a trophoblast, the embryo still remains a sphere without any trace of polarity. When, however, the segmentation cavity appears at some point or other between the trophoblast and the inner cell mass, then the embryo is polarised, and this early polarisation will remain effective during subsequent development. In the Placentalia, again, the morula is surrounded by a zona pellucida and, moving about in the uterine lumen, it is at all sides equally subjected to possible influences emanating from the maternal tissues, and therefore the polarity is the result of forces acting inside the embryo. There is a possibility that, in the Placentalia, some differentiation exists prior to the appearance of polarity, although it does not find a morphological expression. It may be that the segmentation cavity appears at a particular place as a result of previous differentiation. More likely is it that the segmentation cavity may appear at random anywhere between the trophoblast and the inner cell mass. Once this cavity has appeared there is definite polarity. After the embryo has thus acquired a polar differentiation, it attaches itself to the uterine wall in a specific way and in accordance with this polarity.

Different again is the polarisation determined in the early embryo of *Elephantulus*. In this animal the embryo has the form of a hollow vesicle, a blastula. Distinct from the typical blastula of *Amphioxus*, all cells composing its wall are identical, morphologically as well as physiologically. All cells take part in the formation of the inner cell mass, and all cells can produce villi, as normally seen in the early human embryo, although in *Elephantulus* they do this only in abnormal circumstances (van der Horst, 1947). This blastula is lodged, and closely fits, in an embryo-chamber, which, with a somewhat constricted opening, communicates with the main uterine cavity (fig. 9). The greater part of the surface of the blastula, and later of the blastocyst, thus is in direct contact with the epithelium of the embryo-chamber; only a small part freely faces the uterine cavity. This

part subsequently greatly increases in extent to form the thin ectodermal covering of the large yolk-sac. The wall in contact with the chamber epithelium will first become multilayered, and later it will form the ecto-placenta. In this way a polar differentiation is reached. It is not the result of the structural pattern of the egg, nor of forces arising in the embryo itself. Distinct from other mammals, in *Elephantulus* the embryo occupies its definite position in the uterus long before a polar differentiation becomes apparent, and when polarity manifests itself, it appears to be related to the position of the embryo in respect to the uterine wall. It can only be concluded that in *Elephantulus* the maternal tissues induce the polar differentiation of the embryo.

Pre-implantation Reactions.

The pre-implantation phenomena, although they have already been described in a previous publication (van der Horst and Gillman, 1942 *a*), again deserve our attention, as they are closely linked up with the events described more particularly in this paper.

In *Elephantulus*, two stages can be discerned between the moment of ovulation and the time the embryo implants itself in the maternal tissues. The first stage is that of transportation of the egg, and it comprises all events enacted during the period extending from ovulation to the moment the embryo reaches the implantation site. During the second stage the embryo is lodged at the implantation site, but actual implantation, *i.e.* the penetration of the embryonic villi into the maternal tissue, does not as yet occur. Different from *Elephantulus*, these two stages cannot be so clearly distinguished in other placental mammals; they have fused into one, as many events, which take place in *Elephantulus* during the second stage, are already completed during the period of transportation.

Despite the differences in length of the gestation periods of various mammals, the time elapsing between the moment of fertilisation and the arrival of the embryo at the implantation site is, on the whole, remarkably constant. In *Macacus rhesus*, with a gestation period of 164 days (Kenneth, 1947), one can find either a pre-blastocyst in the uterus, or a blastocyst that begins to attack the maternal tissues on the ninth day after fertilisation (Heuser and Streeter, 1941). In man, with a gestation period of 280 days, the embryo has just eroded the uterine epithelium on the seventh day of pregnancy. By contrast, the gestation period of the rabbit is no longer than 31 days on the average, yet the embryo enters the uterus on the third day and only begins to attach itself on the seventh day (Allen, Brambell and Mills, 1947).

It is noteworthy that in all placental mammals, except *Elephantulus*,

the embryo is in the blastocyst stage by the time that it reaches the spot where it will implant itself. Of course the actual length of time, taken up by the transportation, is known in the case of only a few mammals, whereas the developmental stage of the embryo reaching its implantation site has been ascertained in many species. Suffice it to mention that in *Tupaia*, supposed to be the nearest relative of the Macroscelididae, the embryo already consists of 64 to 128 cells by the time it enters the uterus, and, on reaching the implantation site, it is a well-advanced blastocyst (de Lange and Nierstrasz, 1932). It may be concluded that in all these mammals the transportation of the eggs is a slow process.

The probable mechanism of transportation of the eggs in *Elephantulus* has been discussed before (van der Horst, 1943). As timed matings could not be studied, it was not possible to ascertain the exact length of time elapsing during the transportation. However, some conclusions may be drawn from circumstantial evidence. The many series of sections available for study, and the great number of eggs produced by *Elephantulus* at each ovulation, enable us to reach some conclusions.

The transport of the eggs in *Elephantulus* proceeds in two clearly demarcated stages. During the first stage the eggs are transported, probably by ciliary action, from the place where they emerge from the ovary into the ampullary part of the Fallopian tube until they reach the egg-chamber. This first stage undubitably takes rather a long time. Often a good many eggs have already assembled in the egg-chamber, while others are still dispersed over the surface of the ovary or in the folds of the periovarial sac, and some may even still be contained in the Graafian follicles ready for ovulation. How long it takes for each individual egg to reach the egg-chamber cannot be ascertained; it is certain that the progress of each egg through the ampullary part of the tube is a rapid one, yet it takes a long time before all sixty-odd eggs are assembled in the egg-chamber.

In the egg-chamber the progress is definitely arrested. Not a single instance occurs where eggs are already leaving the egg-chamber when others are still on their way towards it. All eggs assemble here before the first one can leave the egg-chamber. So, at least for the first arrivals, the sojourn in the egg-chamber is a rather prolonged one. During this time fertilisation takes place, the second polar body is formed, and the egg undergoes its first, and often its second, segmentation.

The second stage of transportation, from the egg-chamber to the implantation site, seems to be of short duration, and the progress over the rather long distance, therefore, is rapid. The means of transport seems to be the muscular action of the walls of the tube and the uterus. When the early embryo reaches the implantation site it still consists of only four blastomeres, and it is in no way different from an embryo that may be found

in the Fallopian tube. This, in itself, might be the result of a retardation during a possibly long period of transportation, but, in conjunction with two other phenomena, it is more likely an indication of a very rapid transportation.

No less than 68 series of sections with eggs in the egg-chamber are present in the collection. It may happen that all eggs are assembled here; in some cases, however, eggs are still on their way to the egg-chamber, and in others some eggs are already leaving it. By contrast, eggs were found in the isthmic part of the tube, between the egg-chamber and the top of the uterus, only in eight series; and even then only one egg, or a couple at most, are located in this rather long part of the tube. This shows that the eggs pass rapidly, and one by one, through the isthmic part of the Fallopian tube.

When the eggs are in the egg-chamber the uterine lumen is wide open, but as soon as the foremost egg has reached the implantation site, a vigorous contraction of the muscularis sets in, and the lumen above this site is completely closed. Through this action further progress down the uterine horn of the following eggs is prevented. What actually happens is best illustrated by a concrete example. Series 862 contains the beautiful, about 40-celled, blastula lying in the embryo-chamber that is shown in fig. 24. The length of the uterine horn, from its top to the embryo-chamber, is over 8 mm. There are no eggs left in the Fallopian tube, nor are there any in the top part of the horn over a length of 1·2 mm., where the lumen is wide open. All eggs, and they are numerous, are found in the next 2 mm. of the horn in a more or less advanced stage of disintegration. The following 5 mm. of the uterus are tightly contracted, and not a single egg is present in this part. This shows that, at the moment the foremost egg arrives at the implantation site, the distance between it and the next following egg is at least 5 mm. This great distance and the distribution of the eggs in the uterus again indicate a rapid progress of the egg through the uterus.

In *Elephantulus*, therefore, ovulation and the transportation of the unfertilised eggs to the egg-chamber are extended over a rather long period, and the eggs remain in the chamber for a considerable time. But transportation of the early embryo from the egg-chamber to the implantation site is very rapid, and the embryo reaches this place when it consists of four blastomeres only. In other placental mammals, the whole transportation, from the ovary to the site of nidation, is a very slow process, and the embryo reaches its destination when it is already in the blastocyst stage. This difference has a profound effect on the process of nidation.

In all mammals, *Elephantulus* included, the uterus is prepared to receive the embryo when the latter reaches the implantation site. This

preparation apparently requires a certain length of time. The general oedema, so striking a feature of the uterus of *Elephantulus* at the time of ovulation, is not an indication that the uterus is ready to receive the embryo. After ovulation this oedema disappears, and the stroma becomes dark in stained sections. This dark appearance is the result of an enormous increase in the number of nuclei, otherwise there is no difference between the uterus at the time of ovulation and later when the embryo arrives at the implantation site. One might say that by this increase of the nuclei the uterus is under tension. The arrival of the embryo is only necessary to set in motion the whole series of complicated reactions in the uterine wall that have been described. It is probable that in other mammals a similar preparation is necessary. The slow transportation of the early embryo allows the uterus sufficient time to prepare itself for the reception of the embryo. And this time is remarkably constant, independent of the length of the gestation period of the various mammals. Although in *Elephantulus* transportation is rapid, the long duration of the ovulation, and the arresting of the eggs in the tubal egg-chamber, are sufficient to achieve the same result.

On the other hand, the difference in the time of transportation of the early embryo between *Elephantulus* on the one hand, and the other mammals on the other, has a noteworthy consequence. In other mammals the embryo, having arrived at the site, immediately proceeds to implant itself. This is well shown in the golden mole (van der Horst, 1948); also in the macaque the embryonic villi at once grow out from the trophoblast and penetrate into the still healthy uterine epithelium (Heuser and Streeter, 1941). The embryo, in the blastocyst stage, is ready for implantation. In *Elephantulus*, however, the embryo is not yet advanced enough to penetrate the uterine tissues. The 4-celled blastula is already capable of inducing the uterus to undergo a succession of complicated reactions, amongst which the immediate formation of a thimble-shaped embryo-chamber is particularly noteworthy. Such an embryo-chamber is unknown in other mammals, where the embryo attaches itself at once to the uterine wall. In *Elephantulus*, the embryo, although lying free for a considerable time, closely fits in the embryo-chamber and thus is not in danger of being removed from the only place in the uterus where, later on, it can penetrate the maternal tissue. Otherwise the embryo of *Elephantulus* is too immature to make use of the uterine reactions. Only when it is in the blastocyst stage, as in other mammals, does the embryo send out its villi and become fixed to the uterine wall. Thus the uterine reactions are evoked long before the moment of implantation; gradually they gain in intensity, and when the embryo is mature enough for implantation, the swollen uterus is well prepared for its reception. In other mammals the uterine reactions set

in simultaneously with implantation, but, compared with *Elephantulus*, these reactions are then precipitated.

Although the blastula of *Elephantulus* cannot attach itself at the implantation site—and it even appears to be quite independent of this spot as far as its normal food supply is concerned—yet some stimulus arising from the implantation site is necessary for its further development. As said above, the embryo reaches this particular spot in the uterus when it consists of four blastomeres only. A blastula of more than four blastomeres was never found other than at the implantation site. The absorption of fluid by the embryo, once it has started, can continue anywhere in the uterus, resulting in enormously swollen blastulas, but even these consist of only four very attenuated cells (van der Horst and Gillman, 1944). On the other hand, as soon as the early 4-celled blastula has reached the implantation site, further cell division sets in at once. Absorbing more fluid from the uterine cavity, the little vesicle swells up, and simultaneously the number of cells increases, until its wall consists of well over a hundred cells (van der Horst, 1942 *a*). Even then, although it narrowly fits in the embryo-chamber, no direct contact with the maternal tissue is established. Only much later, when the embryo is a well-advanced blastocyst, thus in the same stage as in other mammals, do villi appear and penetrate into the uterine epithelium, and the actual implantation is started.

In most mammals the early embryo, up to the moment of implantation, can continue its development independent from the uterus; or if this influence is required at all it is a diffuse action, emanating from anyhere in the Fallopian tube or the uterus. In *Elephantulus*, on the other hand, not only is the implantation site determined by the uterus alone, but also the early embryo is absolutely dependent from that site for its continued development.

Technique of Implantation.

Not many data are available about the technique of early implantation in the various mammals. In *Sorex* (Hubrecht, 1893; Brambell and Perry, 1946), special crypts are formed by the healthy uterine epithelium into which outgrowths of the trophoblast penetrate; in this way the early embryo is anchored in the uterine wall. Only subsequently the uterine epithelium and deeper tissues are destroyed. Goetz (1937 *a*) found that in *Hemicentetes* the early villi penetrate into the glands and destroy the epithelium, whereas the interglandular connective tissue remains intact for a long time and the capillaries are not opened. Concerning the Carnivora, Fleischmann (1891) says that the primitive villi usually penetrate into the mouths of the glands; whereas Heinricius (1914) maintains that the villi in the dog do not penetrate into the glands but in the tissue between the

glands, and from there they destroy the upper part of the glands; in the cat the villi may penetrate into the glands, but mostly in the tissue between them. In *Elephantulus*, the immediate formation of an embryo-chamber gives some security to the early embryo, and the formation of crypts, therefore, is not necessary. In a way these crypts can be compared with the embryo-chamber of *Elephantulus*. When, in the blastocyst stage of *Elephantulus*, the villi grow out and penetrate into the epithelium, they do not show any predilection for the glands. Occasionally it can be observed that a villus penetrates into a gland, but that is more because it happened to grow out just opposite the mouth. Like the outgrowths of *Sorex* that fit in the crypts, their principle function seems to be to anchor the embryo firmly in the uterine wall. When the villi of *Elephantulus* grow out, the epithelium of the embryo-chamber is already well decomposed. In this respect there exists a noteworthy difference between these villi and those of *Macacus* depicted and described by Heuser and Streeter (1941), otherwise they resemble each other very much. In the latter animal the villi penetrate into the healthy uterine epithelium, and destruction of the uterine tissues between the villi only sets in subsequently. This difference may be related to the age of the embryo. In *Elephantulus* the embryo arrives at the implantation site when it is only a small, 4-celled blastula, whereas in the macaque it is in the blastocyst stage. Also, in *Elephantulus* the villi grow out when the embryo is in the blastocyst stage, so it had time to prepare the ground, which *Macacus* had not.

When in *Elephantulus* the villi have pierced through the basement membrane and penetrated the stroma, again their first purpose seems to be to secure the hold of the embryo. They curve around the swollen subepithelial capillaries without opening their walls. The more these vessels are swollen, the larger is the plasmodial mass surrounding them. The parenchymatous-like tissue, mentioned by Hill (1932) below the region of attachment in *Tarsius*, probably corresponds to this plasmodial mass of *Elephantulus*.

These primitive villi consist of plasmoditrophoblast only, whereas the body of the trophoblast is cellular. When the villi penetrate deeper into the maternal tissue, the plasmoditrophoblast *pari passu* is replaced by cytotrophoblast. In the plasmoditrophoblast mitoses were never found, but in the cytotrophoblast they are of frequent occurrence. Vernhout (1894) also found no mitotic divisions in the plasmoditrophoblast of *Talpa*. The plasmodium gradually is divided up into cells. This also corresponds with Vernhout's description of *Talpa*. He found that the plasmoditrophoblast sends villi into the stroma, but between the villi it disappears, which probably means that here it is transformed into cytotrophoblast, and the latter also penetrates or extends into the villi.

The impression is gained that in *Elephantulus* the plasmoditrophoblast only penetrates into the maternal tissue without transforming it to any great extent, and that the destruction of this tissue through cytolysis is performed chiefly by the cytotrophoblast. The maternal blood-vessels are opened up only when they are reached by the cytotrophoblast. At the implantation site itself the whole plasmoditrophoblast is soon transformed into cytotrophoblast.

Vernhout (1894) found that, in the cytotrophoblast of *Talpa*, lacunae appear that subsequently fuse with the maternal capillaries, and also in *Erinaceus*, according to Hubrecht (1893) and Resink (1903), the maternal vessels join the system of lacunae between the villi. In *Elephantulus*, the swollen capillaries are engulfed first by the plasmoditrophoblast and then by the cytotrophoblast. The original lacunae really are the opened-up capillaries, and a connection of a lacunar system with maternal vessels exists from the beginning. Hill (1932) also found a blood-space between the outgrowing villi in the Catarrhines and, according to Heuser and Streeter (1941), in the macaque the lacunae communicate with the blood-vessels from the outset.

The maternal blood-vessels that are opened by the invading trophoblast are those lying immediately underneath the epithelium of the embryo-chamber. Once this beginning of the placenta has been formed, the cytotrophoblast does not penetrate deeper into the uterine stroma. It is actually prevented from penetrating deeper by the formation of a felt-like layer of very resistant fibres that separates the area of invasion from the deeper layers of the stroma where the decidual reaction sets in. The formation of this layer of fibres was also observed by Goetz (1937 *a*, *b*) in *Hemicentetes* and by Strauss (1943) in *Ericulus*. In these animals the fibrous layer is not very effective; it is formed only during the first stage of implantation, and when, later on, the base of attachment extends, the trophoblast can penetrate into the mucosa of the peripheral area unimpeded.

In *Elephantulus* the original area of attachment hardly extends. The embryo-chamber, originally thimble-shaped, flattens out, but in surface area it hardly becomes more extensive. The placenta, therefore, is always attached to the uterine wall by a narrow base. The fibrous layer in that base remains in *Elephantulus* throughout pregnancy, and is conspicuous when the decidua underneath it has already long since disappeared.

The result of the formation of this fibrous layer, and of the prevention of deeper penetration of the placenta into the mucosa, is that further growth of the placenta can only take place in centripetal direction. It hangs down like a bell in the uterine cavity. This centripetal growth of the placenta was also found by Vernhout (1894) in *Talpa* and by Resink (1903) in

Erinaceus. Hill (1932) also mentions that in *Macacus* the placenta projects into the extra-embryonic coelom.

However, already before this felt-like layer of fibres is well established, the plasmoditrophoblast has penetrated deeper into the mucosa. It grows out in the form of a few deep roots. Most of these roots are profusely branched near their free ends only. Except for penetrating into it, they hardly affect the uterine mucosa. The chief function of these roots, like that of the earlier and shorter plasmoditrophoblastic villi, apparently is to anchor the embryo firmly in the uterus. Once the layer of tough fibres has been formed, the deep roots degenerate and soon disappear altogether; from now on the fibrous layer, connected to the base of the placenta, gives a sufficient hold to the embryo which, moreover, is held in its place by the development of the decidua pseudocapsularis. Vernhout (1894) also describes strands of plasmoditrophoblast in *Talpa* that deeply penetrate into the mucosa and, growing in a centrifugal direction, nearly reach the muscularis. Vernhout, too, is of the opinion that these strands act as anchors. Grosser (1909) mentions long plasmodial roots that deeply penetrate into the maternal symplasma of *Cavia*. The stalk-like prolongation that sometimes grows out in *Tarsius* into the maternal tissue (Hill, 1932) may also correspond to the deep roots of *Elephantulus*. In *Chrysothrix*, the decidua compacta is invaded and even interrupted by more or less extensive, sprout-like prolongations of the trophoblast, that may extend right through it, and in *Cebus*, thick finger-like syncytial processes penetrate deeply into the endometrial tissue in the marginal zone of the placenta. Also, according to Hill, in Catarrhines the trophoblast sends prolongations into the endometrium. All these structures probably correspond to the deep roots of *Elephantulus*. They may occur in other mammals as well. Sections through these roots appear as isolated patches of a plasmodium, sometimes even a section has the appearance of a multicellular giant cell, and the true nature and form of these slender outgrowths can only be determined by carefully tracing them in serial sections or, even better, by making a wax-reconstruction of them.

With the disintegration of the deep roots the last remainder of the plasmoditrophoblast disappears, and as this happens already in the late primary amniotic cavity stage, its existence is only of short duration. As Resink (1903) found in *Erinaceus*, so in *Elephantulus* the whole ectoplacenta is cellular.

Although the placenta soon reaches a considerable size, up to the time that the allantois makes contact with it, it remains a typical ectoplacenta, consisting of trophoblastic elements only. In other mammals the mesoderm may soon penetrate into the villi. Vernhout (1894) found that in *Talpa* the cytotrophoblastic villi soon become hollow and that the mesoderm

penetrates into these cavities. The same can be observed in the golden mole (van der Horst, 1948), in which animal the hollow cytotrophoblast forms a unicellular sheath round a mesodermal core. In the dog the mesoderm penetrates already into the early villi (Heinricius, 1889), and the same happens in monkeys (Hill, 1932). Also in the *Elephantulus* embryo, that was found completely embedded in the stroma, the mesoderm starts to penetrate into the early villi (van der Horst, 1947), but in a normal embryo of *Elephantulus* the villi are formed by the trophoblast only; one can even say the mesoderm never penetrates into them at all.

When the allantois has spread out over the free surface of the placenta, which happens by the time the embryo has formed about 27 pairs of somites, a new period of mitotic activity starts in the placenta. The nuclear divisions, however, are restricted to the neighbourhood of the former free surface of the placenta, now covered by the allantois. This may be an indication that the allantois provides the stimulus for this activity. These newly formed nuclei shift in both directions: towards the embryonic side they help to form the columnar layer of the placenta, and in the opposite direction the nuclei spread out through the thickness of the ectoplacenta. During this process the cell walls in the ectoplacenta are demolished, and a syncytium takes the place of the cells that up till now formed the ectoplacenta. This is a slow process; even in an embryo, 8 mm. long, the cell walls are still present in the deepest part of the placenta near its base; finally, the whole placenta is syncytial, and it remains thus till the end of pregnancy. Hubrecht (1893) and Resink (1903) also mention this disappearance of the cell membranes in the placenta of *Erinaceus*, and Resink correctly remarks that the so-formed syncytium is something other than the plasmoditrophoblast of an earlier period.

These trophoblastic nuclei do not stop at the place of attachment of the placenta, but, penetrating through the felt-like layer of fibres, they enter the maternal mucosa. Also, Strauss (1943) found in *Ericulus* strings of trophoblastic cells penetrating through the fibrous layer; probably they are only nuclei as in *Elephantulus*; and Resink (1903) also mentions strings of cells, probably ectoplacental in origin, in the maternal mucosa.

Whereas the first penetration of the embryo into the uterine mucosa was only superficial, or, as far as it concerns the deep roots, of short duration, and without any serious consequences to the maternal tissues, this second penetration of trophoblastic elements coincides at least with, and may well contribute to, the complete destruction of the decidua.

The Chorion.

Mossman (1937) wishes to reserve the name "chorion" for those parts of the embryonic membranes that are formed by an outer layer of tropho-

blast and an inner, non-vascular, mesoderm; this would mean the outer wall of the exocoelomic cavity. It becomes the allanto-chorion when the exocoelomic mesoderm is replaced by the vascular wall of the allantois.

It has been pointed out that the mammalian trophoblast is homologous with the chorionic ectoderm as found in the reptiles and birds, and that the mammalian yolk-sac is an organ different from the yolk-sac of birds and reptiles (van der Horst, 1945). The superficial ectoderm of the mammalian embryo, no matter whether it is covering the yolk-sac, the exocoelom, or the allantois, or even forms an ectoplacenta, is and remains the same layer of cells, homologous with the chorionic ectoderm of reptiles and birds.

Yet there is something in favour of Mossman's definition. The wall of the exocoelom of the mammals has the same composition as in birds, and is found at a corresponding place. Mossman's definition is acceptable, if it is taken into consideration that the ectodermal layer of this chorion is only a part of the corresponding layer in birds.

It is noteworthy that this thin, non-vascular chorion forms the only connection between the embryo and the placenta before the allantois has established contact with the placenta.

In *Elephantulus* the chorion, the allanto-chorion, as well as the outer wall of the bilaminar or trilaminar yolk-sac, has, on the whole, a smooth surface, and no difference can be observed in the trophoblastic layer between the one and the other (see, however, the section on the placenta, p. 534). Notwithstanding the fact that this membrane is highly active in absorbing the uterine milk, it does not develop villi, or other excrescences, as are often present in other mammals. Only here and there groups of ectodermal cells become elongated, and form nipple-like outgrowths that fit in the mouths of the uterine glands. These outgrowths resemble those described by Weber (1892) in *Manis*. In this animal, however, the elongated cells form a network of ridges on the surface of the allanto-chorion. In *Elephantulus* they form isolated small excrescences. When in the later period of pregnancy the uterine glands have disappeared with the entire endometrium, the surface of the chorion becomes completely smooth.

The Yolk-Sac.

As in the Centetidae (Bluntschli, 1937; Goetz, 1937 *a*), the first divisions of the egg of *Elephantulus* result in the formation of a blastula-like vesicle (van der Horst, 1942 *a*). Although it has the appearance of a typical blastula, as found in *Amphioxus*, this vesicle in *Elephantulus* is not really a blastula; as all the cells of its thin wall are identical, there is, at this stage, no differentiation between an animal and a vegetal pole. This "blastula" is lodged in the thimble-shaped embryo-chamber, where the greater part of

its surface is in contact with the uterine epithelium, and only a small segment faces the opening between the chamber and the uterine cavity.

The way in which the unicellular wall of the "blastula" differentiates into an outer trophoblast and an inner embryonic node and entodermal cells, has been described before (van der Horst, 1942 *a*). Also, it has been pointed out that this unicellular wall can only be regarded as a trophoblast after the formation of the embryonic node. All cells of the "blastula" are morphologically alike, and all contribute towards the formation of the node and entoderm; therefore the whole wall of the vesicle corresponds to the embryonic half of a similar vesicle found in the Marsupialia, and with the yolk, the yolk-ectoderm of the Sauropsida and of the Marsupialia, has completely disappeared in the monodelphic mammals (van der Horst, 1945). In this respect *Elephantulus* is intermediate between the Marsupialia and the monodelphic mammals. The so-called yolk-sac of the mammals, or at least the ectoderm of the bilaminar yolk-sac, therefore, is not identical with the yolk-sac of the Sauropsida. It originates from the small segment of the blastula that faces the uterine lumen.

The difference between the so-called yolk-sac of the mammals and that of reptiles and birds was realised long ago, as appears from the following quotation from Mayer (1834):—

"Gualtherus Needham zerlegte die Eier mehrerer Thiere sehr sorgfältig, machte vortreffliche Beobachtungen über den Bau des Eies, und gab nette Abbildungen (*s. de formato fetu, Londini* 1667.8. *Amstelodami* 1668. 12. *rec. in Mangeti theatr. anat. Tom. II. p.* 537). Bei den fleischfressenden und selbst bei gewissen Nagethieren beschrieb er die *Vesicula erythroides* genauer als die spätern Autoren. Bei dem Eie des menschlichen Weibes behauptet er die Gegenwart einer *Membrana allantoidea*, scheint aber das Nabelbläschen nicht bemerkt, oder mit der *Membrana allantoidea* verwechselt zu haben.

Meckel (*Archiv*, III. Bd. S.5) und E. Weber (Hildebrand's Anatomie, IV. Bd. S.510) behaupten, Needham hätte das Nabelbläschen mit dem Dotter des Vogeleies verglichen, was jedoch nicht ganz richtig ist, indem er nur in Betreff der Gefässe eine Aehnlichkeit zugiebt, aber nicht in Betreff der Bedeutung und Bestimmung. Needham's Worte sind nämlich; '*Adeo ut si recte computemus, vasa vitellaribus respondeant. Humor vero contentus albumini tenuiori, nempe primus in embryonis alimentum facessit et tenellis eiusdem staminibus augendis ac roborandis inservit, donec robustior fiat et crassiori succo digerendo aptior*' " (*Bibl. anat. Mangeti*, P.I. p. 552).

Grosser (1909), on the other hand, is of the opinion that the large size of the mammalian yolk-sac is an important indication that once it contained a large amount of yolk. With the yolk it lost its function, and it is now to be regarded as a functionless organ inherited from the mammalian ancestors, although it may often acquire a new function in a secondary way.

The mammals, that lost the Sauropsidian yolk-sac with the yolk,

developed a new organ, the so-called yolk-sac, or better, umbilical vesicle, and this organ has an important function to fulfil during the first stage of pregnancy. The food of the embryo consists at that time predominantly, or even exclusively, of uterine milk. When the trophoblast, covering the yolk-sac, destroys the uterine wall, as, for example in *Orycteropus* (van der Horst, 1949 *c*), it gets a histiotrophic function as well.

When the embryo becomes completely embedded in the uterine stroma, and thus is cut off from the supply of uterine milk, the yolk-sac is no longer a nutrient organ; it remains small and changes its character completely as in man, and in one embryo of *Elephantulus* that abnormally became completely embedded (van der Horst, 1947). In *Gymnura* and *Erinaceus*, although the embryo is also shut off from the uterine cavity, the umbilical vesicle still plays an important rôle according to Hubrecht (1898 *a*). But in these animals the embryo really becomes enclosed in a niche of the uterine cavity, into which open a good number of glands. In *Cavia* and some other rodents the yolk-sac has gone to the other extreme. By the breaking down of the outer wall of the yolk-sac, the entoderm is directly exposed to the surrounding nutrient mass and, as said by Sansom and Hill (1931), this entoderm plays an important rôle in the absorption of food. This is reminiscent of a starfish everting its stomach completely and thus digesting and absorbing the body of a mussel. Yet the eversion of the entoderm in these rodents occurs rather late in development and, as pointed out by Heuser and Streeter (1941), the still intact yolk-sac is small in the blastocyst stage and its trophoblastic wall remains relatively thick. On the other hand, in the rabbit, pig and monkey, which are not wholly, or not at all, interstitial in their implantation, the yolk-sac is already well distended by the time the embryo is in the blastocyst stage.

The same can be observed in *Elephantulus*. Once the early blastocyst is anchored in the epithelium of the embryo-chamber, the small area of its surface, not in contact with the epithelium, starts to grow vigorously, and soon protrudes as a large sac into the uterine cavity. Gérard (1923) lays some stress on what he supposes to be the natural form of the yolk-sac in *Nasilio*, where he found a wider distal part connected by a narrow canal with the part adjoining the embryo proper. This form, however, is due to a collapse, as may easily occur during fixation with such a thin-walled vesicle. If fixed in its natural position the yolk-sac of *Elephantulus*, and no doubt of *Nasilio* as well, is a large round vesicle the thin wall of which is closely applied to the uterine epithelium. Through its thin, bilaminar wall the yolk-sac absorbs the fluid, nutrient material secreted by the active uterine glands. Although the embryo is well fixed in the uterine wall by this time, and even the placenta is already a conspicuous organ, it is most likely that during the first period of pregnancy, as long as the allantois

has not yet established contact with the ectoplacenta, the yolk-sac is the main, if not the sole, organ for feeding the growing embryo. The yolk-sac is already a voluminous organ before its wall is supplied with blood-vessels at all. When later, by the development of the exocoelom, the stalk is reduced to a narrow canal, the omphaloidean circulation undoubtedly plays an important rôle in conveying the food from the yolk-sac to the embryo; but these blood-vessels are not necessary for the absorption of the uterine milk. In several mammals the omphaloidean vessels never extend over the whole surface of the yolk-sac. In *Elephantulus* these blood-vessels reach the abembryonal pole of the trilaminar yolk-sac just before the entoderm is completely detached from the trophoblastic ectoderm by the intervening exocoelom and allantois. This happens when the embryo has reached a length of about 6 mm. From now on the yolk-sac really is an umbilical vesicle; its wall, richly vascularised, consists of entoderm and the splanchnopleura only. By this process the absorption of uterine milk from the uterus is not interrupted. It can readily be assumed that the trophoblast continues with this function, and that the absorbed food is deposited into the allantois instead of in the yolk-sac (see next section). Neither is it likely that the yolk-sac is itself reduced to a functionless remnant directly it is detached from the trophoblast. Brambell and Perry (1946) found that, in *Sorex* and *Crocidura*, the yolk-sac remains an important absorptive organ throughout development, and, according to Grosser (1909), the yolk-sac of the Chiroptera develops and possibly serves till the end of pregnancy for the absorption of the food from the exocoelom surrounding it. Also in *Tarsius*, as Hill (1932) says, the yolk-sac plays a highly important rôle in the nutrition of the embryo, at least during the earlier part of the gestation period. In *Elephantulus*, like in *Erinaceus* and *Talpa* (Resink, 1903), the yolk-sac shrinks to a folded organ; its mesothelium is composed of large cells, as Hill found also to be the case in *Tarsius* and *Cebus*. It is probable that this richly vascularised wall continues in *Elephantulus* to convey the absorbed food from the exocoelom to the embryo, at least for some time, until the placenta is fully established.

The Allantois.

In the early primitive streak stage *Elephantulus* has a connecting stalk, consisting of an accumulation of mesodermal cells, connected to the posterior end of the embryonic disc. This rudiment of a stalk has the same appearance as the early connecting stalk described by Hill (1932) in *Tarsius*. Whereas in the latter animal, as well as in monkeys and man, this stalk develops in a permanent embryonic structure conveying the allantoic vessels to the placenta, in *Elephantulus* it is of a very temporary nature,

and the accumulation of mesodermal cells is hardly noticeable already in the late primitive streak stage (van der Horst, 1944 *a*). That this accumulation of cells represents a connecting stalk is shown not only by its similarity to that of *Tarsius*, but also in an embryo of *Elephantulus*, showing interstitial implantation, the same structure leaves no doubt about its identity. It consists of a hollow entodermal core, surrounded by a sheath of mesoderm and connected to the caudal end of the yolk-sac (van der Horst, 1947). The peripheral end of this stalk is already in contact with the chorion, and its mesodermal cells start to invade the chorionic villi. In every respect this stalk corresponds to that described in man. Whether it also corresponds to the definite body-stalk of *Tarsius* is open to doubt, as will be shown in the section on the placenta (p. 534).

When the embryo of *Elephantulus* has developed 8 somites, the definite allantois makes its appearance again as a mesodermal thickening at the posterior, ventral side of the embryo, into which a small entodermal diverticulum penetrates. In an embryo with 14 somites it forms a conspicuous structure hanging down into the extra-embryonic coelom (fig. 44). In some way or other it swings round the side of the embryo, and establishes contact with the placenta, when the embryo has 18 somites. In this respect *Elephantulus* seems to be slightly more precocious than other mammals; in *Ericulus* the allantois has just reached the placenta when the embryo has 23 somites (Strauss, 1943), and in a *Loris* embryo with 22 somites the allantois is still a small vesicle protruding into the extra-embryonic coelom (Hill, 1932).

Even so, when the allantois of *Elephantulus* establishes contact with the ectoplacenta, the latter is already a fairly large structure. De Lange (1933) has pointed out that the original place of the placenta is in no way determined by the allantois; this is clearly shown by *Elephantulus*. Somehow the outgrowing allantois is attracted by the placenta, and so vigorously does it swing round to reach the placenta, that the posterior part of the embryo is turned on its side. Before this, the dorsal side of the embryo is facing the placenta; when the allantois establishes contact with the placenta, the embryo is twisted, and anteriorly the dorsal side is still facing the placenta, but soon the whole embryo turns on its side in respect to the placenta.

When the allantois reaches the placenta it has the form of a cylinder, except that it is bent. The base at once spreads out over the inner surface of the placenta, so it gets the form of a cone; and when the embryo has 27 somites the edge of the allantois has reached the periphery of the placenta. During this process the inner wall of the allantois, separating it from the exocoelomic cavity, becomes extremely thin, but the outer wall, applied to the placenta, is thick and vascular. In this respect the allantois of

Hapale, as described by Hill (1932), is intermediate between that of *Elephantulus* and the solid connecting stalk found in other monkeys and man; in *Hapale* the allantois has a flattened cavity, one wall of which is extremely thin.

As soon as the allantois has covered the whole inner surface of the placenta it continues to spread like a thin curtain, separating first the exocoelom from the trophoblastic ectoderm (fig. 18), and then penetrating, simultaneously with the exocoelom, between the yolk-sac entoderm and the trophoblast. Although the allantois remains a narrow cavity it becomes very extensive in this way, and finally it surrounds the embryo, the yolk-sac and the exocoelom completely, being everywhere in direct contact with the trophoblastic ectoderm. The yolk-sac and its blood-vessels are thus replaced by the allantois and the umbilical vessels, and this change in the circulation is no doubt of great importance for feeding the foetus. This change is effected in *Elephantulus* when the embryo is about 6 mm. long.

The same phenomenon has been observed in other mammals, with a noteworthy modification. Goetz (1937 *b*) mentions that in *Centetes*, the peripheral branches of the umbilical vessels grow out beyond the allantois, and vascularise the circumplacental chorion; only in a later stage does the allantois follow its vessels and extend to the ob-placental pole. According to Hill (1932), the allantoic vessels in Lemurs spread out between the peripheral lobes of the allantois, until the chorion is entirely vascularised by allantoic vessels at a time when the allantoic cavity is still small. In *Tarsius* the development of the allantois is accelerated, and at the same time abbreviated, so as to enable it to vascularise the placental area of the chorion directly and at the earliest possible moment. Hill is of the opinion that the allantois of the Lemur, the connecting stalk of Tarsius and the stalk of the higher Primates, represent three stages in an evolutionary series. Two more stages, preceding that of the Lemur, could be added to this series. In *Elephantulus* the allantoic vessels spread out simultaneously with the allantois; in *Centetes* the vessels precede the allantois but are later followed by the allantois; in the Lemur the vessels extend beyond the allantois, and the latter remains relatively small; in *Tarsius* only the allantoic vessels in a mesodermal stalk grow out to the pole opposite the embryo, and the same happens, with some reservation (see section on the placenta), in monkeys and man. This implies that an extensive, although not voluminous, allantois is a primitive feature in mammals.

The Placenta.

According to Grosser (1909), placentation is the intimate connection (Aneinanderlagerung oder Verwachsung) of the uterine mucosa with the

chorion, that is vascularised by way of the allantois or yolk-sac. Flynn (1923) gave this definition: "The term 'placenta' should be applied to all organs consisting of an intimate apposition or fusion of the foetal membranes with the uterine wall for the purpose of carrying out physiological processes destined for the well-being of the embryo. This may be an allanto-placenta, a vascular and a non-vascular omphalo-placenta." Flynn's definition is wider than that of Grosser, even if we accept that the intimate connection of Grosser can also mean a close apposition, and in my opinion it is more satisfactory. Grosser makes the reservation that the structure must be vascularised in order to be considered a placenta, but according to Flynn the yolk-sac placenta, at least, can be non-vascular. Vascularity does not seem to me to be a necessary attribute of a placenta. In an 8 mm. embryo of *Orycteropus* there is an allanto-placenta and, separated from it, a very complex omphalo-placenta (van der Horst, 1949 *c*). The former is well supplied with embryonic blood circulating in a rich network of umbilical vessels. But the maternal tissue in contact with it shows only a very few slightly dilated capillaries. The uterine epithelium here is eroded, and nobody would hesitate to classify this structure as a syndesmo-chorial placenta. In the region of the omphalo-placenta the large trophoblastic cells have destroyed not only the uterine epithelium, but they have also eaten their way deep into the stroma, leaving intact, however, a rich network of swollen maternal capillaries between them. But here there are no embryonic blood-vessels at all. Yet this structure undoubtedly is an endotheliochorial omphalo-placenta. This tends to show that blood-vessels, either maternal or foetal, are not necessarily an attribute to a placenta, although their presence makes the structure more effective. Any fusion or intimate apposition of the foetal membranes with the uterine wall for the purpose of feeding the embryo can be considered as a placenta. Again some objection may be raised against the use of the word "feeding". Reasons will be given why the complicated structure, associated with an embryo of *Elephantulus* with 14 somites (fig. 44), does not feed the embryo, at least not directly. Yet nobody would hesitate to call it a haemo-chorial placenta. I do not know if Flynn had such a case in mind when he used the words "for the well-being of the embryo", but in any case they serve the purpose.

According to de Lange (1933), the chorion originally forms the placenta without any reference to the allantois, and the connection with the allantois is only established when the placentation is well under way. In several animals it can be observed that a placenta is initially formed in the yolk-sac area, and no doubt it functions effectively before the allantois establishes a connection with it. In *Elephantulus* the haemo-chorial placenta is being formed when the yolk-sac practically fills the whole blastocyst, and is also applied to that part of the trophoblast where the placenta is in the process

of formation (fig. 12). Next the yolk-sac in the placental area is replaced by the exocoelom, which apparently does not make any difference in the growth of the placenta (fig. 14), and finally when the embryo has developed 18 somites, the allantois makes contact with the placenta. This contact has a great influence on the placenta, certainly, yet one cannot admit that before the moment of contact it was not a placenta at all.

If we adhere to Grosser's definition of a placenta, and, for a stronger reason, if that given by Flynn is accepted, then *Elephantulus* simultaneously has two placentas, each of a totally different type. There is, in the first place, a well-developed and circumscribed haemo-chorial placenta, at first supplied with maternal blood only (fig. 15). Later the allantoic circulation is added (fig. 19). Yet the large yolk-sac also functions as a placenta and can only be regarded as an epithelio-chorial placenta. It is closely applied to the uterine wall, and it absorbs the food supplied by the uterine glands. If accidentally an embryo is cut off from this food-supply, it is literally starved to death (van der Horst, 1949 *a*). At first this yolk-sac placenta is non-vascular (fig. 14), then it is progressively supplied by the omphaloidean vessels (figs. 15, 17). Finally the yolk-sac itself is separated from the outer surface by the penetrating allantois, and the yolk-sac vessels are replaced by the allantoic circulation (fig. 19). It has now become an allantoic placenta. From the beginning it forms an epithelio-chorial placenta in a very primitive form.

The presence of more than one type of placenta simultaneously in a particular animal can often be observed, were it only in the form that in many mammals with a haemo-chorial placenta the allantoic vessels extend beyond this placenta into the chorion laeve (Goetz, 1936). In this respect the Centetidae are particularly noteworthy. According to Goetz's description (1937 *b*), a central placenta olliformis is surrounded by a labyrinth placenta. The circumplacental chorion further destroys the maternal tissue and the obplacental chorion laeve at least destroys the uterine epithelium; so here we have a typical syndesmo-chorial placenta and partly an endothelio-chorial placenta, supplied by allantoic vessels.

In *Potamogale*, Hill (1938) found a diffuse placenta involving the whole of the uterine decidua, except for a small disc where a haemo-chorial placenta is formed. Normally the placenta of the Lemuroidea is of the epithelio-chorial type, but in *Galago demidoffi*, Gérard (1929) found an area in an otherwise normal placenta where the uterine epithelium was broken up by histolysis and the chorion was in direct contact with the connective tissue; thus in this species there seems to be an epithelio-chorial placenta and a syndesmo-chorial placenta as well.

In this connection it is also noteworthy that in both the Insectivores and the Primates there are forms with an epithelio-chorial placenta only and

others with a haemo-chorial placenta. Nearly all Insectivores have a haemo-chorial placenta. The diffuse placenta of *Potamogale* has been mentioned already. In the American mole, *Scalopus aquaticus*, Mossman (1939) found a primitive epithelio-chorial placenta with short villi penetrating into uterine crypts, from which he rather hastily concluded that the original Insectivores had such an epithelio-chorial type of placenta, and that all groups with this type of placenta may form a base-line from which the other groups have developed.

Grosser (1909) gave his well-known classification of placentas, and later (1936) says that the sequence, epithelio-chorial, syndesmo-chorial, endothelio-chorial and haemo-chorial, is a phylogenetic one, starting with the most simple form and ending with the most complicated. Hubrecht (1908), on the other hand, is of the opinion that the diffuse placenta of Ungulates and Lemurs is not primitive, but derived from the haemo-chorial type by simplification. Other authors, Assheton (1909), Flynn (1923), Wislocki (1929) and de Lange (1933), in general agree with Hubrecht's contention. Hill (1932), however, holds views precisely opposite to those of Hubrecht. According to Hill, the Lemuroid placenta is the progenitor of that of higher forms, and suggests that the occurrence of this non-deciduate type of placenta in such diversely related groups as the Lemuroidea, the Ungulates, etc., is not to be explained by any hypothetical process of simplification, but by the persistence of the ancestral type without any essential modification. He considers *Tarsius* to form a transition from the primitive Lemuroid to the specialised Pithecoid type.

I cannot agree either with Hubrecht or with Hill. *Elephantulus* has two types of placentas simultaneously, the highest and the lowest form of Grosser, and both are active in the nourishment of the developing embryo. There is no transition between them either—the one is clearly demarcated from the other. Moreover, there are grounds for accepting that both placentas represent primitive forms in their respective types. The extensive epithelio-chorial placenta of *Elephantulus* has no accessory structures; except for a number of small papillae during some part of its existence, it has a smooth surface, closely applied to the uterine epithelium. But it is well supplied with omphaloid or allantoic blood-vessels and, according to all definitions, it must be regarded as a placenta, albeit of a very primitive type. I agree with Hill that the haemo-chorial placentas of *Tarsius*, the Platyrrhines, the Catarrhines, and man, represent an ascending line of phylogenetic development. There is reason to accept that the haemo-chorial placenta of *Elephantulus* represents another step downwards in this row (see section on the placental circulation). I prefer to compare the epithelio-chorial placenta of *Elephantulus* with the same type of placenta found in Lemuroids and other mammals, and the haemo-chorial placenta

of *Elephantulus* with other haemo-chorial placentas. I do not see any reason to compare a haemo-chorial placenta of higher Primates or lower Insectivora with something that is not present at all in the Lemurs, or for that reason in other mammals.

A haemo-chorial placenta starts its existence with the destruction of the uterine tissues through the cytolytic action of the trophoblast. It has been pointed out before that this cytolytic potential can be confined to only a part of the trophoblast and that its existence can be of short duration. If it is suppressed altogether, which might mean the loss of a single genetic factor, no penetration can take place, and no haemo-chorial placenta can be formed. The embryo must find ways and means to make good the loss. That an embryo can readily adapt itself to a change in its environment is shown by the embryo of *Elephantulus* with interstitial implantation. All representatives of the Insectivora are known to have a haemo-chorial placenta. In the mole *Scalopus* it is suddenly absent. Moreover, amongst the Talpidae, which themselves are a more advanced family of the Insectivora, *Scalopus* is not considered to be primitive (Weber, 1928). This absence of the haemo-chorial placenta in *Scalopus* can only be explained by a sudden loss.

When comparing the epithelio-chorial placenta of *Elephantulus* with that of the Lemuroidea it is found that the latter shows a great advance over the former. In *Loris*, rounded chorionic villi fit into a honeycomb-like system of crypts in the endometrium (Hill, 1932); in *Chiromys*, the chorion has rather complex villi interdigitating with outgrowths of the uterine mucosa (Hill and Burne, 1922). The importance of this placenta with its outgrowths for the nourishment of the embryo is shown by the precocious vascularisation of the chorion by the allantoic vessels (Hill, Ince and Subba Rau, 1928). In general, it can be said that whenever the loss of the more complex type of placenta lays a more onerous burden on the simpler epithelio-chorial placenta, the latter increases its surface by the development of more or less complicated villi. On the other hand, when a complex placenta is present, the chorion, although active, remains smooth. In man and other mammals with interstitial implantation, the epithelio-chorial placenta has been completely reduced. When we take into consideration that an epithelio-chorial placenta, as a rule, is present concomitantly with a placenta of a more complex type, the sudden loss of either the one or the other becomes understandable in various and widely divergent groups of mammals, and this loss is accompanied by the acquisition of a more complex and effective form of the remaining placenta.

There is reason to accept that a close relation exists between the position of the haemo-chorial placenta of the Insectivora and the Primates, and the way in which it is formed, on the one hand, and in the method of amnion

formation on the other. Not always, however, does this relation exist. When, as in the Chrysochloridae (van der Horst, 1948), the embryo implants itself in the lateral wall of the uterus and the placenta is formed at this place, whereas the embryonic disc is mesometrial or antimesometrial, then no direct relation between placentation and amniogenesis can be demonstrated. But when the embryonic disc and the place of implantation are orientated in the same direction, both being mesometrial or antimesometrial, then such a relation certainly exists.

In *Elephantulus* both the amnio-embryonic vesicle and the early placenta are orientated towards the mesometrial side of the blastocyst. The amnion is formed by cavitation, and from the beginning the amnio-embryonic vesicle is and remains separated from the trophoblast that forms the placenta (fig. 12). Hence the placentation is not influenced by the proximity of the embryonic disc nor by the formation of the amnion. In this respect the monkeys are in close correspondence with *Elephantulus*; they also form the amnion by cavitation. In both, the formation of the placenta is apparently not affected by the presence of the amnio-embryonic vesicle at the same side of the blastocyst.

In *Sorex* also the embryonic disc and the placenta are orientated towards the same side; here both are antimesometrial (Hubrecht, 1893). But the embryonic disc is not covered over by the trophoblast, it is exposed, and the amnion is formed by folding. It is clear that the placenta cannot be formed on the area of the embryonic disc. Correspondingly, the placenta, at first, has the form of a ring surrounding the disc. When the amnion is formed by folding, the placenta, *pari passu* with the closure of the amnion folds, extends towards the centre, and finally it forms a complete cap. The same has been observed in *Talpa* (Vernhout, 1894). The position of the two lateral haemo-chorial placentas of *Tupaia*, also, may be explained by the exposed embryonic disc and the amniogenesis by folding.

This relationship between amniogenesis and the formation or the position of the placenta may shed some light on the position of the placenta of *Tarsius*.

In several monkeys a second placenta is formed at the place where the blastocyst comes into contact with the opposite wall of the uterus. Hill (1932) gives the following summary. The placenta is double in *Nasilio*, it is usually double in *Macacus*, but occasionally single in *M. rhesus* and in *M. cynomolgus*; in *Semnopithecus* it is also normally double; in *Papio* the placenta is single. A double placenta is usual in *Cebus*, *Ateles* and *Chrysothrix*; in *Mycetes* it is normally single and in *Hapale* it is always single. In man the placenta is always single, but occasionally a double placenta occurs, as was already mentioned by Saint-Ange (1844). As far as this can be ascertained from the position of the amnio-embryonic vesicle, the

single placenta, or the first when the placenta is double, corresponds in position with the single haemo-chorial placenta of *Elephantulus*.

In *Tarsius* the placenta is situated opposite to the embryonic disc. It may be concluded that this placenta of *Tarsius* corresponds to the secondary placenta of the monkeys, and that the formation of the primary placenta cannot be achieved, because in *Tarsius* the embryonic disc is exposed and the amnion is formed by folding.

Elephantulus also has a secondary placenta, although it is only rudimentary. Attention has already been drawn to the fact that the chorion does not affect the uterine epithelium of the bursa embryonica, neither has this epithelium an influence on the structure of the chorion, in so far as its ectoderm remains a simple unicellular layer of cells throughout. However, when the decidua pseudocapsularis is opened, and the embryonic membranes come into direct contact with the epithelium of the main uterine cavity, the chorionic ectoderm suddenly increases in thickness and becomes multilayered. This part of the chorion has been described as the rudimentary secondary placenta. It has exactly the same appearance as the area of thickened ectoplacental trophoblast of *Semnopithecus* figured by Hill (1932) and by Grosser (1909) after Selenka. Although this thickening of the chorion in *Elephantulus* is evident only when the embryo is already rather large, viz. about 6 mm., whereas the *Semnopithecus* embryo of Selenka is only in the blastocyst stage, yet the similarity, both in structure and in position, is so evident that no doubt can be raised against the homology. In *Semnopithecus* this thickening is the first indication of the formation of the secondary placenta. In *Elephantulus*, therefore, the same structure can only be considered to be a rudimentary secondary placenta.

The short duration of this thickening of the chorion is remarkable. It is present only when the embryo is from 5 to 8 mm. long; before and after that time the ectoderm consists only of a unicellular layer. In this respect the erratic occurrence of the secondary placenta in the monkeys is worth noting, and the question arises whether the secondary placenta of many monkeys might also bé represented by a temporary thickening only. Anyhow, in *Elephantulus* an abortive attempt to form a second placenta can be observed. In this respect *Elephantulus* approaches the monkeys much closer than *Tupaia* or any other mammal does.

Although no solution can be offered, yet the question why, or under what influence, this abortive secondary placenta is formed at all in *Elephantulus* should be considered. It arises rather suddenly when the bursa embryonica is forced open by the growing embryo and thereby the chorion comes into contact with the antimesometrial wall of the main uterine cavity. Moreover, the thickened chorion closely corresponds in extent with the newly exposed surface of the main uterine cavity, whereas along the lateral

sides, where the remains of the bursa embryonica can still be discerned, the chorionic epithelium remains as thin as it was before (fig. 19). This might indicate that the antimesometrial uterine wall induces this vigorous growth in the chorion. The uterine wall, however, does not show a corresponding reaction. Also the antimesometrial uterine wall is structurally different from the mesometrial side, where the primary placenta is formed. It is, therefore, not likely that the uterine wall induces the chorion to form a secondary placenta.

It is remarkable that exactly the opposite can be observed in golden moles. In this animal the embryo fixes itself in one of the lateral walls of the uterus, and the placenta will be formed here. The opposite lateral wall often shows a decidual reaction, but this is not answered by a corresponding reaction of the trophoblast, as far as could be ascertained provisionally, and only one lateral placenta is formed.

On the other hand, the secondary placenta of *Elephantulus* becomes apparent when the allantois has extended to the antimesometrial side of the embryo, and here the yolk-sac circulation has been replaced by the allantoic vessels. When the allantois has reached the primary placenta, it here induces a renewed growth of the trophoblastic tissue to form the columnar layer of the placenta. Similarly, the allantois might induce renewed activity in the trophoblastic ectoderm at the obplacental pole of the embryo. In *Tarsius* also the secondary placenta is formed as soon as the allantoic stalk has reached the appropriate place. It is, therefore, more likely that the allantois provides the necessary stimulus rather than that the uterine wall does it.

There remains the question why only a rudiment of the secondary placenta is formed, which, moreover, is evident only during such a short period. The columnar layer of the primary placenta, which constitutes the main feeding mechanism of the embryo, is formed after the allantois has reached the placenta. In an embryo with 27 somites it is still very rudimentary (fig. 17), and even when the embryo is 4·9 mm. long it is not yet sufficiently established (fig. 18). In an embryo of 6·14 mm. length (fig. 19) it is already so far developed that it can be assumed that it functions efficiently. It might be possible that the secondary placenta is already redundant shortly after it makes its first appearance. Maybe the erratic occurrence of the secondary placenta in monkeys can be explained in a similar way.

The Glands.

All uterine glands have exactly the same appearance in *Elephantulus* at the time of oestrus; they are equally distributed, and no part of the

uterus, neither in the cross-section nor along the longitudinal axis, is devoid of glands. Yet only a very few glands, those directly related to the implantation site, react when the embryo arrives. They swell up enormously in their deeper part, and assume a spiral course nearer the uterine lumen. Thus these glands become very conspicuous (figs. 7, 8), yet they are few in number; also they do not branch as Gérard (1923) supposes to be the case in *Nasilio*. Later, some more glands start to swell, until the embryo is completely surrounded by a sphere of swollen glands.

Towards the antimesometrial side of the uterus the glands do not swell up in such a conspicuous way. Apparently they are actively engaged in the secretion of uterine milk for feeding the embryo. Although the embryo is surrounded by the decidua pseudocapsularis, there remains an opening in the centre through which the glandular product can reach the bursa embryonica from the main uterine cavity (fig. 15). This is in marked contrast to what has been observed in *Erinaceus* and *Gymnura* (Hubrecht, 1898 *a*). In these animals the embryo is enclosed in a separate part of the uterine lumen. The glands, opening in this chamber, are very active, but in the rest of the uterus they are reduced, and a great part of the glandular tissue disappears. Different also is the situation in the bat *Glossophaga soricina*, where, according to Hamlett (1935), the glands in the decidua basalis, that are closed off by the placenta, are completely reduced. In *Elephantulus* the glands underlying the placenta remain widely open; whether they function in the usual way or not is another question. When in *Elephantulus* the main uterine cavity is stretched out enormously after the reduction of the decidua pseudocapsularis, the small glands of the antimesometrial wall of the uterus are completely opened up and they can no longer be recognised as glands (fig. 19). But the epithelium, that of the uterine cavity as well as that of the original glands, becomes very high, with tall columnar cells, and it can be assumed that it continues to secrete actively.

In mammals with an epithelio-chorial placenta, the glands are the principal source of food for the embryo; Hill (1932) found the uterine glands in *Lemur* very active during the entire period of gestation. In mammals with a haemo-chorial placenta the glands play an important rôle, at least in most of them. Man also has a haemo-chorial placenta, but here the interstitial implantation cuts off the embryo completely from the glandular product. The embryo meets this situation by the precocious establishment of a very extensive haemo-chorial placenta. This was shown by an *Elephantulus* embryo that accidentally became completely embedded in the uterine stroma (van der Horst, 1947). In the same way as in a normal human embryo, it had sent out villi over the entire surface of the trophoblast, and these villi had already established intimate contact with the maternal

blood, although the embryo was only in the primitive streak stage. The normal twin brother, or sister, of this abnormal *Elephantulus* embryo looked like the one here shown in fig. 14, with an ectoplacenta that does not feed the embryo directly and with a large yolk-sac that absorbs the uterine milk.

The fact that the uterine glands provide all the necessary nutrition for the embryo during the earlier stages of development is also shown by an abnormality, occasionally found in *Elephantulus*. It may happen that, instead of one, two embryos arrive at the implantation site. As there is room for one only, the second lies on top of the first, and thus shuts off the first embryo from the main uterine cavity. Although the first embryo can get all the benefits of the decaying wall of the embryo-chamber, only the second can send out its yolk-sac and absorb the uterine milk. The first is literally starved to death and the second will survive.

Also Hill (1932) says that in the Platyrrhines there can be no doubt that the epithelium of the uterine glands is a highly important source of histiotrophic material.

In *Elephantulus* the uterine glands are the main, if not the only, source of nutriment to the embryo during the first half of pregnancy. During this period, lasting about four weeks, growth in bulk is slow; at the end the embryo has reached a crown-rump length of only 4 mm. At the end of the fourth week of pregnancy, the allantoic circulation in the placenta has developed to such a point that the placenta can gradually take over the feeding of the embryo (fig. 18). This does not mean that feeding by uterine milk comes to an abrupt ending. The transition is gradual. It may even be that at first the nutrition by the glands increases in intensity, when the allantois completely surrounds the embryo, and the yolk-sac circulation, underneath the chorion, is replaced by the allantoic vessels (fig. 19). The period during which the embryo is fed by uterine milk could not be established; it may extend until the end of pregnancy. However, at the end of the first half of pregnancy the placenta starts to function as the main source of food for the embryo. Growth in bulk then becomes more vigorous, and during the second half the embryo increases its length from 4 mm. to 4 cm.

Moreover, up to the time the embryo measures 4 mm. or slightly more, the somites can readily be counted; their number is then just over forty. More somites will be added to the tailend, but all of a sudden the anterior somites start to grow out, and they can no longer be recognised individually. This is also an indication of a sudden change in the growth-rate at the moment that the placenta replaces the yolk-sac as the main feeding mechanism of the embryo.

The Decidua.

At the time of oestrus the uterus of *Elephantulus* shows a general stromal oedema, and the epithelium is very high. This oedema is confined to the posterior part of the uterine horn, where it occurs all round, and no difference can be detected between the lateral, mesometrial or antimesometrial walls (fig. 3). This oedematous appearance is in marked contrast to the dense stroma and the low epithelium found during the period of anoestrus (fig. 2). The gradual transition from the anoestrus to the oestrus state has been described before (van der Horst, 1946). Attention has also been drawn to the great mitotic activity at the time of oestrus (van der Horst and Gillman, 1942 *a*). This results in an enormous increase in the number of nuclei, and, in stained sections, the uterus has a dark appearance at the time the embryo arrives at the implantation site (fig. 4). It looks as if the uterus had reverted to a stage of dark stroma, such as exists during anoestrus, with this difference, that the epithelium remains high as it is during oestrus. A more careful study, however, reveals a great difference between the dark stroma stage and that of anoestrus. The diameter of the uterus is already much larger during the dark stroma stage than during anoestrus, and it is of the same dimension as during oestrus. The nuclei are very small during anoestrus, they swell considerably at the approach of oestrus, and in the following dense stroma stage they retain the same large size. But they are very crowded, and correspondingly the vacuoles are small. The uterus, at the dense stroma stage following ovulation, is prepared to receive the embryo; it is, so to speak, under tension, and the arrival of the embryo is all that is needed to set in motion the chain of reactions that follow each other during pregnancy. When the embryo has arrived at the implantation site a new oedema appears in the stroma. To distinguish this from the oestrus oedema it may be designated as the pregnancy oedema. Distinct from the oestrus oedema it is localised and restricted to the mesometrial pole of the uterus, where implantation will occur. The pregnancy oedema later spreads, but it will never involve the whole of the lateral walls of the uterus, and even less the antimesometrial side.

This occurrence of two stages of oedematous stroma, different from each other, and separated by the stage of dense stroma, shows that the oestrus oedema itself is not an indication that the uterus is ready to receive the ovum; it is only the means to that end.

The early decidual reaction follows shortly after the appearance of the pregnancy oedema. It is noteworthy that both the pregnancy oedema and the decidual reaction first become apparent in the immediate neighbourhood of the embryo-chamber; from here they spread like waves to the periphery. This indicates that the stimulus for these succeeding reactions emanates

from the embryo-chamber, it may be directly from the embryo itself, or from the wall of the chamber after this has appropriately been stimulated by the embryo.

The decidual reaction at first affects all stromal cells in the same way; they all assume a typical pear-shape, and the vacuoles become smaller. In the early blastocyst stage of the embryo and before actual implantation, a differentiation starts to take place, and the future giant cells can be recognised between the pear-shaped cells. This early decidual reaction and differentiation of the cells is noteworthy. When, finally, the embryo is so far developed that it can send out its villi to penetrate the uterine tissues, the decidual reaction is already well advanced (figs. 31, 32). In other mammals, *e.g.* the golden mole (van der Horst, 1948) or the macaque (Heuser and Streeter, 1941), the embryo is much further developed than in *Elephantulus* by the time it reaches its implantation site, and it immediately sends out its villi into the uterine epithelium. At that moment a decidual reaction then becomes apparent, but compared with *Elephantulus* it is precipitate.

Gigantism of cells in the mammalian pregnant uterus is a remarkable phenomenon, and it has been mentioned by many authors. These giant cells may be of embryonic origin, as they undoubtedly are in the rabbit (Sansom, 1927), in *Orycteropus* (van der Horst, 1949 *c*), or in *Sorex* (Hubrecht, 1893). In some cases the origin of the giant cells is questionable; in man and other primates they are maternal cells. In *Elephantulus* there are no embryonic giant cells, but they form a most conspicuous feature of the maternal tissues. They first appear in the neighbourhood of the embryo-chamber; from there their formation spreads throughout the decidua compacta and spongiosa, through the muscularis and into the mesometrium in the later part of pregnancy, where they can be found a good distance away from the uterus. At the same rate at which they appear towards the distal side, they are broken down nearer the centre, so that by the end of pregnancy the giant cells are found only in the mesometrium some distance from the uterus (van der Horst and Gillman, 1946 *b*). The same distribution of the giant cells, both in rate and position, was found by Gérard (1922, 1923) in the related *Nasilio*.

In *Elephantulus* the giant cells reach their peak of development in the decidua compacta by the time the embryo has about thirteen somites, *i.e.* before the allantois has established contact with the placenta. By this time a great number of them are already destroyed. This destruction may take place *in situ*; generally the giant cells are removed by way of the decidual arteries. Their remains can be found in the lacunae of the ecto-placenta (fig. 64, *o*). Resink (1903) found such deciduofracts in the ecto-placenta of *Erinaceus*. The large, endothelial cells found by Hill (1932) in

Macacus and *Nasalis*, that often become detached and block up the lumina of the vessels, are probably decidual cells. In *Tarsius*, apparently, the decidual giant cells are destroyed in the same way as in *Elephantulus*, and taken by the maternal blood to be stranded in the placental lacunae, although Hill is of the opinion that the giant cells form an integral part of the ectoplacenta, and are a remarkable feature in the growth of the trophoblastic mass. Hubrecht (1898 *b*, 1899) thought that their chief rôle is that of providing nuclei destined to give origin to maternal red blood corpuscles. Nitabuch (1887) describes how in the human uterus the endothelium of the arteries can be interrupted, where large cells protrude in the lumen or the endothelium may still cover these large cells; sometimes she found large cells lying free in the lumen. This has also been observed in *Elephantulus*. According to Goetz (1936), the large cells, surrounding the coiled arteries in the decidua of *Centetes*, are derived from muscle-cells, these swollen cells being contractile and regulating the flow of the blood in the placenta. No doubt the many large cells protruding in the coiled arteries of *Elephantulus* influence the flow of the blood, and may even block the vessels altogether, but they are certainly not derived from muscle-cells.

As Fujimura (1921) has shown, the giant decidual cells are glandular, but for the rest their function is left in doubt. Gérard (1923) is of the opinion that the product contributes towards feeding the embryo; Fujimura is inclined to believe that the substance is absorbed by the mother and not by the embryo.

In *Elephantulus* many giant cells are already destroyed, and their remains are removed by the placental circulation before the allantois makes contact with the ectoplacenta, and thus before the placenta directly feeds the embryo; the last giant cells in the mesometrium disappear only after parturition (van der Horst and Gillman, 1946 *b*). This indicates that the product of these glandular cells is carried away by the blood-stream, to be absorbed by the mother. On the other hand, there remains the remarkable fact that, in their distribution, the giant cells are closely bound to the maternal arteries. In the decidua compacta this is not so conspicuous, but in the muscularis and the mesometrium the giant cells form a regular sheath around the arteries. The wall of the veins, on the other hand, is completely devoid of giant cells. So their product must always pass the placenta first, before it can possibly act on the mother, which is a noteworthy arrangement.

The Destruction of the Decidua.

The destruction of the mucosa is initiated, in *Elephantulus*, by the breaking up of the thin septa between the swollen glands in the peripheral

part of the endometrium. This process was also described by Gérard (1923) in the nearly related *Nasilio*.

The breaking down of the interglandular septa starts when the embryo is only in the primitive streak stage, and it is confined to the periphery, near the muscularis. It is, therefore, a process quite independent from the real, and complete, destruction of the mucosa that first becomes apparent in the centre, near the attachment of the placenta.

By this disappearance of the interglandular septa, the swollen parts of the glands become confluent and now form a continuous space between the muscularis and the decidua; thus the decidua compacta and spongiosa, surrounding the embryo and the placenta, become detached from the muscularis, except where the blood-vessels pass into the mucosa.

The epithelium lining the peripheral side of the swollen glands, and covering the inner aspect of the muscularis, remains intact, and its cells assume a high columnar form. This epithelium now forms a continuous layer. No matter what happens in the more central part of the mucosa, this conspicuous epithelium remains intact during the whole period of gestation. After parturition it will form the new lining epithelium of the uterine lumen. In this way the necessary steps have already been taken during early pregnancy to ensure the reconstruction of the uterus after parturition.

Similar phenomena have been described for a few other mammals. In the rabbit, Sansom (1927) found that the deeply situated portions of the uterine glands form a layer of cubical cells, which escape destruction, and persist even though giant cells pass through it. In *Chrysothrix* (Hill, 1932) the glands are greatly enlarged, and their basal portions are lined by an intact epithelium; also in *Cebus* the basal parts of the swollen glands have a columnar epithelium in later pregnancy.

The complete destruction of the decidua starts in the compacta, and spreads from there in a peripheral direction, until nothing is left between the embryo and the healthy glandular epithelium, discussed above, but some detritus. The last elements to disappear are the trophoblastic nuclei that had previously invaded the mucosa. In the end, the only connection of the placenta and embryo with the uterine wall is formed by the three placental arteries and the single vein. In *Sorex* too (Hubrecht, 1893), when the placenta is fully formed, the maternal tissue between it and the muscularis is reduced to a layer of debris. This destruction of maternal tissue in *Elephantulus* is confined to the decidual tissue at the mesometrial side of the uterus. At the antimesometrial side, where no decidual reaction ever takes place, the uterine wall is simply stretched so that the glands are completely opened and flattened out, but the original uterine epithelium remains intact, and connects up with the high epithelium of the peripheral

wall of the glands, and together they will form the new epithelium of the uterus after parturition.

The Coiled Arteries.

The coiled arteries of the uterus are known also under the name of spiral arteries or arterioles, and Turner (1873), and long before him J. Hunter (1787) and W. Hunter (1777), used the term "curling arteries". J. and W. Hunter, and even earlier Väter (1725) and Noortwyk (1743), were the first to direct attention to these remarkable structures, according to Waldeyer (1890). Reading through a rather extensive literature, it can only be concluded that these arteries are even more remarkable in *Elephantulus* than in any other mammal in which they are known to occur.

The occurrence of coiled arteries in the uterus of the various mammals is in itself already striking. Yet one has to be careful in this respect. The mere fact that an otherwise careful author does not mention them, when describing the phenomena of pregnancy, is no indication that they are absent. Both Hubrecht (1889) and Resink (1903) do not mention coiled arteries in their work on *Erinaceus*, yet in the South African hedgehog they are present, so most likely they are present in the European hedgehog as well. So only those cases can be mentioned in which their presence or absence has been definitely stated. Amongst the Insectivores they are found in *Elephantulus* and *Nasilio* (Gérard, 1923), in *Centetes*, *Hemicentetes* (Goetz, 1936, 1937 *b*) and *Ericulus* (Strauss, 1943). As mentioned above, they occur in the South African hedgehog, *Erinaceus frontalis*. On the other hand, they are absent in the golden mole, *Eremitalpa*, in *Suncus*, and probably in the other Soricidae, as well as in *Talpa*. According to Branca (1927) there are no coiled arteries in *Vespertilio*. Remarkable is their occurrence in *Choloepus*, for which animal Turner (1873) gave an accurate description of the curling arteries, accompanied by beautiful illustrations. The endometrial arteries, supplying the yolk-sac placenta of *Orycteropus*, show at least one characteristic in common with the coiling arteries of *Elephantulus* (see below). Otherwise these arteries are only found in Primates, although not in all. Most likely they are absent in the Lemuroidea, and their presence in *Tarsius* is at least not mentioned by van Herwerden (1905). According to Kaiser (1947 *b*), coiled arterioles are absent in the endometrium of the New World monkeys, *Cebus*, *Ateles* and *Alouatta*, investigated by him. Yet he found two types of endometrial arterioles in these Platyrrhines, and one type proceeds on a relatively straight course, without branching, almost to the superficial epithelium. Although these arterioles are not coiled, the fact that they run, without branching, almost to the superficial epithelium seems to indicate that they represent a simpli-

fied form of the coiled arteries. Typical coiled arteries were found in the Catarrhines, Macacus and Papio, by several authors (Daron, 1936; Herberg, 1934, *et al.*) and according to Kaiser (1947 *a*) they are present in the chimpanzee and the gibbon as well. The coiled or curling arteries in the endometrium of the human uterus have been known long since. Waldeyer (1890) gives a summary of the older literature on this subject.

Summarising our present rather scanty knowledge, it can be said that coiled arteries occur in the Macroscelididae (*Elephantulus* and *Nasilio*), the Centetidae (*Centetes*, *Hemicentetes* and *Ericulus*), and the Erinaceidae (*Erinaceus frontalis*), *i.e.* in the more primitive families of the Insectivora, and then again in the monkeys, apes and man. Their presence in *Choloepus* is surprising.

Spiral arteries have been described in other organs, for example by Reynolds (1947 *a*) in the ovary of the rabbit. Although these spiral arteries superficially resemble the endometrial coiled arteries, they are different structures altogether in their form as well as in their function; for which reason it is better to call the latter not spiral but coiled or curling arteries, even if they may have the form of a regular spiral as those figured by Turner in *Choloepus*. As described by Reynolds, the spiral arteries extend and contract with the changing size of the ovaries, due to the temporary presence of ripe follicles or corpora lutea. When they are extended, the coils are flattened and at a greater distance from each other, as is always the case in a spiral. Moreover, in Reynolds' figures a distinct turning-point in the spiral can be observed, such as occurs in the tendrils of a vine. The presence of such a turning-point indicates that the artery was straight at first, and that it assumed the form of a spiral only after its peripheral end was fixed. In the coiled arteries there is not such a turning-point even when they have the form of a regular spiral, as is clearly shown in Turner's figures, and extension of the uterus has not the same effect on the coiled arteries as swelling of the ovaries on the spiral arteries. From the figures of Kaiser (1947 *a*) it appears that the artery is by far more intricately coiled in the swollen endometrium of the secretory phase than in the thin endometrium of the proliferative phase of the uterus. The very drastic changes of the coiled arteries in the uterus of *Elephantulus* during pregnancy, resulting in their complete obliteration, clearly indicates that structurally and functionally they are different from the spiral arteries that, without further change, simply extend and contract.

The striking features of the coiled arteries of *Elephantulus*, as compared with those of other mammals, can be summarised as follows:—

(1) They arise from the myometrial arterial network independently of the other endometrial arteries.

(2) The connection between the myometrial arteries and the coiled arteries is and remains extremely narrow even when the coiled arteries are greatly swollen.

(3) The coiled arteries are few in number; usually there are only three of them.

(4) Over their entire length the coiled arteries have no side branches.

(5) The coiled arteries are very long and follow a very irregular course not at all in the form of a spiral, first in the decidua spongiosa, and then in the peripheral part of the decidua compacta.

(6) The last section, in the central part of the decidua compacta, is nearly straight, and remains narrow when the convoluted part has already swollen considerably during the first part of pregnancy.

(7) All three coiled arteries converge towards the centre of the attached placenta, where usually two of them fuse to form one of the two central placental arteries, the third coiled artery being continued into the second placental artery.

(8) With the destruction of the decidua compacta and then of the decidua spongiosa, the very long coiled arteries are reduced in length over their whole extent, from where they enter the decidua to the point where they are continued into the central placental arteries. They become short and wide canals that run in a straight line from the myometrium to the centre of the placenta.

(9) The single placental vein and these three straight arteries form the only connections between the foetus and the uterine wall during the later part of pregnancy.

(10) At birth these vessels are severed near their base in the myometrium, from where they grow out again as new coiled arteries during the restitution of the uterus.

The accumulation of decidual cells around these arteries and their penetration into the arterial lumen have been discussed in the section on the decidua.

1. The myometrial arteries branch repeatedly in *Elephantulus*, and it is only from one of the smaller end branches that the coiled arteries arise. In the human uterus, however, the endometrial arteries arise directly from the main stems of the arcuate arteries. Kaiser (1947 *a*) gives a schematic representation of the vascular elements of the human uterus. According to him, the endometrial artery first gives off some branches that branch in the usual way in the deeper part of the endometrium; they are the basal arteries, and only then the main stem assumes the character of a coiled artery. Waldeyer (1890), on the other hand, maintains that the

coiled arteries in the human uterus can be discerned already in the muscularis and that branches are practically absent. In *Elephantulus* the coiled arteries are already distinct from the other endometrial arteries before they enter the endometrium, whereas, if Kaiser is correct, this separation in man only occurs in the deeper part of the endometrium. Also Daron (1936) found that in *Macacus rhesus* the coiled artery enters the mucous membrane as a continuation of a rather straight radial artery in the myometrium, which in turn springs directly from the stratum vasculare.

2. The connection between a myometrial artery and an enormously swollen coiled artery was found to be so narrow in *Elephantulus* that it could be identified only with some trouble. This very narrow connection is also mentioned by Goetz (1936) for *Centetes*, in which animal he found the lumen of the coiled artery much wider than its connection with the artery in the muscularis. In *Macacus*, according to Daron (1936), the radial arteries that are continued into the endometrium as the coiled arteries, are constricted as they pass through the inner fourth of the myometrium. He usually found a very abrupt change in the diameter of the lumen as the artery passes from the myometrium into the endometrium, as in *Elephantulus*. Daron is of the opinion that these constrictions must greatly reduce the blood-flow to the coiled arteries. The endometrial arteries that supply the yolk-sac placenta of *Orycteropus* also are greatly constricted where they emerge from the wider arteries in the deeper layer of the mucosa, and in this respect at least these arteries correspond with coiled arteries. On the other hand, such a narrow connection does not seem to exist in the human coiled arteries.

3. The small number, and the constancy of that number, of coiled arteries in the uterus of *Elephantulus* is remarkable. Practically always there are three of them, once only two and rarely four were found. Moreover, it can be stated with confidence that these three arteries are the only ones present over the entire length of each uterine horn of *Elephantulus*. As far as can be ascertained, *Elephantulus* is unique in this respect. Strauss (1944) figures an indefinite number of coiled arteries over the whole length of the uterine horn of *Ericulus*. In the South African hedgehog a great number of coiled arteries are related to each placenta, and this animal bears several young ones in each litter. Turner (1873) also figures a large number of coiled arteries in *Choloepus*. In monkeys and man the placenta is supplied by a large number of coiled arteries.

4. A characteristic of the coiled arteries of all mammals is that they have no side branches. In one specimen of *Elephantulus* two coiled arteries were found that bifurcated, but each branch pursued its way as a normal coiled artery. Daron (1936) also mentions a few cases of bifurcation in *Macacus*. In this animal the arteries give rise to very few branches;

many that were carefully studied had none. Kaiser (1947 *a*) also pictures a single side branch to the coiled arteries of man, although Waldeyer (1890) says that they do not branch. According to Herberg (1934), the coiled arteries of *Macacus* give off a few capillaries, but otherwise they do not split up. Goetz (1936, 1937 *b*) also mentions that in *Centetes* and *Hemicentetes* the coiled arteries are not branched. Thus, as Daron remarks, the bulk of the blood is carried well towards the surface epithelium before passing into capillaries. Immediately deep to the uterine epithelium the coiled arteries divide abruptly into numerous small capillaries. Kaiser (1947 *b*) found that one type of endometrial arteries in the New World monkeys proceeds, without branching, almost to the superficial epithelium. Although in these monkeys this type of artery pursues a relatively straight course and therefore does not really deserve the name of coiled artery, the fact that it goes without branching through the whole thickness of the mucosa is sufficient reason to identify this type as a coiled artery of a simple form.

5. Turner (1873) gives a figure of a coiled artery of *Choloepus* in the form of a perfect spiral. Otherwise these arteries have a more or less irregular course, although short spirals may intervene between irregularly twisted parts. In *Elephantulus* nothing like a spiral could be detected, and over its whole length the artery is twisted and curved in a most irregular fashion. It has already been said that the vessel, believed to represent the coiled artery in the Platyrrhines, follows a nearly straight course. Also in the macaque the artery is relatively simple; judging from the figures given by Kaiser (1947 *a*), about half a dozen coils may occur in its course. Also in the hedgehog and in the Centetidae the number of coils is limited. In man the artery seems to be more complicated; Waldeyer (1890) mentions that in 5 to 6 square mm. of a section, one and the same vessel may be cut 15 to 20 times. Even this is by far surpassed by the coiled arteries of *Elephantulus*, as can be seen in figs. 14 and 67; but it is only after one has spent one or two days tracing the course of a single artery in all its meanderings, that the most complicated pattern of this course can be fully appreciated. Consequently the length of the artery is really enormous in comparison to the distance in a straight line from the point where it enters the mucosa to its junction with the central placental artery.

6. The final part of the coiled artery of *Elephantulus* runs in a nearly straight course through the innermost portion of the decidua spongiosa. Nitabuch (1887) also found that the very last part of the arteries in man is straight. When, during early pregnancy, the coiled artery of *Elephantulus* is already considerably swollen and very conspicuous in sections of the uterus, this last part is still extremely narrow and, although it is nearly

straight, it is very difficult to follow its course to where it ends in the swollen lacunae underneath the epithelium of the embryo-chamber. This very narrow portion of the otherwise conspicuous coiled artery presumably also occurs in the macaque. In this animal Heuser and Streeter (1941) found no evidence that the spiral arteries enter into the lacunae. The blood received or returned by the lacunae, according to these authors, appears to be limited to that passing through the abundant large openings into the venous plexus, as indicated in (their) fig. 3. They end their description with the curious sentence: "All endothelial vessels apparently join up with the venous network, with the sole exception of the spiral arteries." Their fig. 3 correspondingly shows the coiled artery ending blindly, somewhere in the mucosa.

7. It is a peculiar sight to see two large blood-vessels join in the pregnant uterus of *Elephantulus*, and to see them splitting up again a little distance beyond (fig. 16). Gérard observed the same in *Nasilio*; maybe all elephant shrews will show it. How this fusion of two decidual arteries at the point of entry into the placenta came about has been explained on p. 493. The third coiled artery also comes into close proximity to the point of fusion of the other two, but it remains independent along its course through the centre of the placenta. Although in other animals as well as in man the coiled arteries tend to enter the central region of the placenta, their entrances are spread out, nevertheless, over a considerable area of the placenta, and every artery remains separate from the others. In the Centetidae the coiled arteries are arranged in a circle around the central blood-space, and in the hedgehog the points of entry are spread out more irregularly over the outer surface of the placenta.

8. In *Elephantulus* each artery follows its meandering course through the whole decidua spongiosa and the greater peripheral portion of the decidua compacta. This seems also to be the case in monkeys and man. In the hedgehog, on the other hand, the convolutions are restricted only to the peripheral part of the mucosa, just inside the muscularis, and also in the Centetidae the coils seem to be restricted to the deeper part of the mucosa. Consequently, when in *Elephantulus* the decidual tissue is destroyed in mid-pregnancy, the coiled arteries are affected over their whole length. This destruction starts near the base of the pedunculated placenta, and spreads from there in a peripheral direction. The arterial wall, however, is not destroyed; it is even strengthened by the addition of a layer of strong fibres. *Pari passu* with the destruction, the coiled artery becomes surrounded by a symplasma, and later just by some debris; its coils are contracted and the artery is transformed into a straight vessel.

9. The three arteries and the one vein finally form the only connection between the placenta and the uterine wall; the placenta and the foetus are

then suspended by the walls of the four vessels, radiating from the narrow base of the placenta.

10. At birth these vessels are severed, or anyway undergo complete destruction. All that is left of the coiled arteries after birth is a small stump embedded in the very thin layer of mucosa. With the restitution of the mucosa the new coiled arteries grow out from these stumps. How far the destruction of the coiled arteries extends in monkeys and man, and if some part of the arteries escapes destruction, is unknown to me. Anyhow, during menstruation only the end part of the artery is destroyed, and the coils of the basal portion remain intact (Kaiser, 1947 *a*). In *Ericulus*, as Strauss (1943) says, the coiled arteries, surrounded by large decidual cells, remain intact till the end of pregnancy, and after parturition the basal portion of the coiled artery remains, but its wall becomes sclerotic (Strauss, 1944); this also happens with the mesometrial and the myometrial artery in *Elephantulus* (van der Horst and Gillman, 1946 *b*). Judging from its position during early pregnancy, it seems likely that in the hedgehog also the coiled artery is not entirely destroyed.

The coiled arteries of *Elephantulus* can only be recognised as such when, during the first part af pregnancy, they are swollen. In the non-pregnant animal they are so narrow that they cannot be seen at all in the sections, or when visible they cannot be traced in subsequent sections and, therefore, cannot be identified with certainty as coiled arteries. For this reason some doubt may arise whether they are present at all in the non-pregnant animal, in which case one could presume that they are only formed, or that they adopt their meandering course, when the early embryo has reached the implantation site. However, when one takes into consideration that, when the embryo only is in the blastocyst stage, these arteries are sufficiently swollen to follow their course from beginning to end in serial sections, and that then it can be definitely established that they follow at least the same, if not a more intricate, course as later on when the embryo is in the primitive streak stage, then it is justified to assume that they are coiled also before they are well visible. Moreover, in *Ericulus* (Strauss, 1944) the coiled arteries can be identified as such during dioestrus, and in the macaque they remain clearly visible during the whole menstrual period (Kaiser, 1947 *a*).

Accepting that the coiled arteries are present in the non-pregnant *Elephantulus*, but that through their narrowness they cannot be identified or distinguished from other endometrial arteries, one might ask again where they should be located. In a previous section (p. 505) it has been explained that in *Elephantulus* only a narrow segment of the uterine wall is directly affected by the arrival of the early embryo at the implantation site, and that only this part, in the form of an inverted cone, swells to a relatively enormous size. Considering this fact in relation to the position of the coiled arteries

in the pregnant animal, one can conclude that in the non-pregnant animal the three coiled arteries are situated near the surface of the cone, and that the equally narrow, decidual vein occupies approximately the centre.

This cone forms only a small part of the endometrium at the mesometrial side of the uterus, in cross-section as well as along the longitudinal axis. The rest of the endometrium, also, is well supplied with arteries which, in suitable material, can be seen running mainly in a radial direction and giving off side branches anywhere. They conform to the second type of endometrial arteries found by Kaiser (1947 *b*) in the Platyrrhines, which pursue a relatively straight course until they disappear, presumably into the capillary bed, at various levels in the thickness of the endometrium.

The occurrence of two different types of arteries and their distribution in the endometrium of *Elephantulus*, is illustrated in an obvious and remarkable way. At oestrus the endometrium is very oedematous over a considerable length of the uterus, and in cross-section the oedema extends all round the uterus. Moreover, this oedema arises simultaneously in the whole thickness of the endometrium. Soon after ovulation this oestrus oedema disappears, and the endometrium is dense when the embryo arrives at the implantation site. Then a new oedema makes its appearance, but this pregnancy oedema appears first just underneath the uterine epithelium, from where it gradually extends towards the periphery, and, moreover, it is restricted to the surroundings of the embryo-chamber at the mesometrial side of the uterus. The lateral and antimesometrial uterine wall retain their dense stroma. It seems that these two different types of oedema are in some way or other related to the two types of uterine arteries, and maybe the conclusion is warranted that the general uterine arteries are affected by oestrogen, whereas the coiled arteries are sensitive to progesterone only.

Phelps (1946) came to the same conclusion in experiments with the rhesus monkey. In this animal, as found also by Daron (1936), there are two types of endometrial arteries, the large coiled arteries and the small straight arteries; the latter extend only in the basal zone of the mucosa. The coiled arteries were found to be affected by progesterone, resulting in a rich blood-supply just under the endometrial surface at the time the developing ovum is ready to implant. This author assumes that the essential action of progesterone, without which nidation cannot take place, is wholly or in part its action upon the endometrial vascular bed.

It has been pointed out before (p. 500) that in *Elephantulus* there is only one very small and circumscribed area of the uterine wall where implantation can take place. It has also been mentioned that the three coiled arteries, coming from different directions, converge towards the implantation area. It may therefore be concluded that the implantation site is determined by the coiled arteries, or more accurately, by the place where the otherwise

unbranched coiled arteries finally split up into capillaries just underneath the uterine epithelium. There may be other factors that help to determine the implantation site, or the convergence of the coiled arteries, in turn, may be caused by some other factor, but the only factor that up till now could be recognised is that represented by the coiled arteries and their endings.

In an earlier publication (van der Horst and Gillman, 1942 *a*) it has been mentioned that in *Elephantulus* it is possible, although not likely, that the implantation site can shift over a length of 1 or 2 mm. in each uterine horn during subsequent pregnancies. Strauss (1944) refers to this when he wants to show that such a shifting is of general occurrence in mammals. However, further study has shown that in *Elephantulus* the implantation site remains at the same place in subsequent pregnancies. The provision has to be made that, except for a very narrow basal strip, the whole endometrium of *Elephantulus* is destroyed during pregnancy, and with it the coiled arteries, and after parturition the endometrium is completely restored and new coiled arteries are formed. In this sense a completely new implantation site is formed. There is, however, an indication that the new site is on the same place as the old one. The base of the coiled arteries in the myometrium remains, and can be readily identified from one pregnancy to the next one by the thick sclerotic walls. In the next pregnancy it proves to be again the base of the new coiled arteries in the endometrium (van der Horst and Gillman, 1946 *b*). Strauss may be right when he maintains that in *Ericulus* the new implantation sites alternate with the old ones, but whether the old sites are not well fitted for nidation, because the sclerosis of the arteries results in a diminution of the blood-supply, seems open to doubt. In *Elephantulus*, anyhow, the sclerotic arterial walls do not form such an impediment, and during a subsequent pregnancy they are completely transformed, so that no difference in the constitution of the arterial wall between a primipara and an older animal can be detected.

When there are a great number of coiled arteries in the endometrium, as in the hedgehog, the Centetidae and the Primates, they may not play such a decisive rôle in determining the implantation site as in *Elephantulus*, and especially in the hedgehog and the Centetidae with their large litters this seems unlikely, yet in monkeys and man there seems to be at least a predilection for certain areas of the uterine wall; in *Macacus*, according to Heuser and Streeter, the location of implantation is rather definitely regulated.

That in *Elephantulus* there exists a definite relation between the coiled arteries and the implantation site is shown in one slightly abnormal case. Besides the three normal, swollen coiled arteries in this animal, another, seen in the sections, was conspicuous by its narrower lumen. On being

traced, its course was found to be much less intricately tortuous than that of the normal arteries. This narrow, coiled artery did not end at or near the centre of the embryo-chamber, but just underneath the edge of the healthy uterine tissue in the neck of the embryo-chamber. Herberg (1934) mentions smaller coiled arteries in the macaque that could not be followed in the sections to the intervillous space of the placenta; these small arteries are perhaps similar to the aberrant one in *Elephantulus*.

Finally, a possible relation between the presence of coiled arteries and menstruation may be considered. That such a relation exists in Catarrhines is known from the work of Daron (1936), Kaiser (1947 *a*) and others. In *Macacus*, according to Daron, the large coiled arteries are directly involved in the progravid and menstrual changes of the mucous membrane. Thus, while in the proliferative phase the arteries only extend, roughly, through the basal half of the endometrium, in the late progravid phase arterial fields and terminal arterial branches are found immediately underneath the surface epithelium. The region of the mucosa, which suffers no damage during menstruation, represents the potential capillary bed of the simple arteries of the second type. Kaiser (1947 *a*) also found that the coiled arteries of the macaque undergo characteristic alterations during the menstrual cycle. It has already been said that the first type of endometrial arteries, found by Kaiser (1947 *b*) in the Platyrrhines, may represent a simplified type of "coiled" arteries, although they are not really coiled. It is noteworthy, in this respect, that menstruation in the Platyrrhines is microscopic in amount, so Kaiser does not need to modify the hypothesis that alterations of the coiled arterioles are responsible for menstruation. On the contrary, the Platyrrhines show that there is close correspondence between the coiled arteries and menstruation.

In *Elephantulus* the same correspondence is evident, in so far as menstruation, although very vigorous, is restricted to the small area of the mucosa where the coiled arteries are situated. Our knowledge of other animals concerning this question is quite insufficient. In some animals, like *Tarsius* (van Herwerden, 1905) or the bat *Glossophaga soricini* (Hamlett, 1934), menstruation is known to occur, but one is left in doubt whether they have coiling arteries; in others, like the Centetidae (Goetz, 1937 *b*; Strauss, 1944), and in the South African hedgehog, coiled arteries occur, but it is unknown whether they menstruate in some way or other or not.

There is even more doubt about the function of these remarkable decidual arteries. Daron (1936) says: "Leopold (1877) suggested that the very tortuosity of the endometrial arteries would greatly retard the flow of blood through the vessels. What we know of the flow of fluids through tubes justifies this conclusion." He also mentions the abrupt change in the diameter of the lumen, as the artery passes from the myometrium

into the endometrium, and is of the opinion that these constrictions must greatly reduce the blood-flow to the coiled arteries and their terminal capillary beds. Such constrictions occur in *Elephantulus* too, but they do not seem to be universal. Goetz (1937 *b*) and Kaiser (1947 *a*) also express the opinion that the coiled arteries are of great importance in regulating the amount of blood that may pass through them. It is not clear in what way these enormously swollen arteries, with their apparently rather rigid walls, can regulate the flow of the blood (see, however, p. 540).

Whereas the decidual arteries are very complex and most remarkable structures, the venous system in the decidua shows nothing in particular to distinguish it from other veins. As Herberg (1934) found in the macaque, so in *Elephantulus* all venous branches from the placenta unite with the branches in the decidua, and finally they all fuse to a single vein in the muscularis.

The Placental Circulation.

When using the term "placental arteries" in *Elephantulus*, one has to be well aware of the fact that, strictly speaking, the two vascular canals, running in the axis of the placenta, are not arteries at all. As explained previously, they are nothing else but elongated lacunae that have not even a wall of their own, let alone a muscular layer, but they are surrounded by ectoplacental tissue. Yet, as far as the placenta is concerned, they play the rôle of arteries, conveying the maternal blood, branching up into smaller vessels, and finally into a very narrow network that may be compared to a capillary system, from where the blood again is reassembled into real veins, viz. the decidual veins.

These two placental arteries are the continuation of the three coiled arteries, present during the first period of pregnancy, and of the three straight arteries, into which the coiled arteries have been transformed at a later period. This transformation of the decidual arteries has no direct effect on the placental arteries.

The two placental arteries run parallel to each other in a straight line in or near the axis of the placenta from its attached peduncle to the embryonic surface of the placenta, where they split up into a number of radiating vessels. During the earlier period of pregnancy these radiating vessels are embedded in the substance of the placenta, although very near the surface; later on they become more detached, and can be seen radiating and repeatedly branching on the embryonic surface of the placenta. From these radiating vessels numerous very fine canals arise that pervade the placenta, and collect again into a number of wider veins at the attached placental peduncle. These veins occupy here a more peripheral position, whereas the arteries

are in the centre. The maternal blood, therefore, percolates through the placenta from the embryonic to the maternal surface.

The same general direction of the maternal blood-flow has been observed in various mammals by different authors. In bats this arrangement seems to be general. Nolf (1895) says that the arterial capillaries penetrate into the placenta of *Vespertilio* from the inside and the veins emerge at the outside. Grosser (1909) confirms this, and also de Lange (1933) mentions that the placental arteries go through the placenta to the foetal side and the veins arise from the outside. This was also found by Branca (1927), and Hamlett (1935) saw the arteries penetrate to the foetal side of the placenta in South American phyllostomid bats. In the South African hedgehog with a placenta similar to that of *Elephantulus*, the placental arteries could be followed right through the thickness of the placenta to the embryonic side, and the veins emerge at the outer surface. Also in *Procavia* the maternal blood is conveyed through wide maternal channels to the inside of the placenta and, percolating through the placental network, it is collected into veins at the outside (Sturgess, 1948). According to Jenkinson (1904), the maternal arteries of the Muridae pierce the placenta in the centre and branch on its foetal side, whereas the veins arise at the basal side. In this respect the Centetidae are somewhat puzzling. In *Ericulus*, Strauss (1943) found the maternal arteries going right through the placenta to the embryonic side, from where the blood enters the lacunar system. This is in conformity with what was found in the other mammals mentioned above. On the other hand, according to Goetz (1936, 1937 *b*), in *Centetes* and *Hemicentetes* the arterial blood enters the lacunar system at the maternal side of the placenta towards the centre, and the veins emerge at the same side towards the periphery. This is the more remarkable as, in another respect (*vide infra*), the placenta of *Ericulus*, as well as that of *Centetes* and *Hemicentetes*, shows a close resemblance to that of *Elephantulus*.

In the Primates with their placenta olliformis it is more difficult to ascertain the direction of the maternal blood-flow through the placenta. According to Nitabuch (1887), the arteries in man open into the intervillous space at the convex surface of the placenta, and the veins have their origin along the margin; the blood, therefore, runs from the centre to the periphery. But Hill (1932) found that in *Chrysothrix* the maternal placental arteries pass through the villous system as huge capillaries, and then proceed to divide a short distance below the chorion, whereas the veins take their origin from the large spaces abutting on the peripheral syncytium. The arrangement in *Chrysothrix*, therefore, is more in conformity with that of other mammals. Maybe in other Primates also "arterial" blood-spaces connect with "venous" spaces only near the internal surface of the placenta.

Very few data are available in the literature about the direction of the

embryonic circulation in the placenta, although several authors give information about the position of the allantoic vessels. This is not surprising. Especially during the first part of pregnancy, when the embryonic blood can readily be distinguished from the maternal blood on account of the nucleated erythrocytes, it is not very difficult to certify whether the placental capillaries contain maternal or embryonic blood. But it is difficult to make certain about the direction of the embryonic blood in the placenta, as it is hardly, if at all, possible to distinguish between the arterial and the venous branches of the allantoic vessels that lie intermingled on the embryonic surface of the placenta. Even if this can be done, it is nearly impossible to trace the capillary system between the arteries and veins. In the literature only four statements could be found concerning the direction of the embryonic blood in the placenta. All are identical. Mossman (1926), Mossman and Weisfeldt (1939) and Strauss (1943) say that the maternal and foetal blood stream in opposite directions respectively in the rabbit, in the ground squirrel and in *Ericulus*, and Barcroft and Barron (1946) found in the placenta of the sheep that the maternal and the embryonic blood flow parallel to each other but in opposite directions.

Considerable attention was paid to the problem. The study of the embryonic circulation in *Elephantulus* is facilitated because, in the first place, the embryonic blood penetrates into the placenta only to a certain well-demarcated level. In this part of the placenta, the columnar layer, the maternal and foetal capillaries run parallel to each other and at right angles to the embryonic surface of the placenta. In the second place, this layer of columns is traversed in a diagonal direction by much wider embryonic vessels. These diagonal vessels may either convey the blood to the columnar layer or collect it from the parallel capillaries, depending on the possible direction of the circulation. Now these diagonal embryonic vessels could be traced, and this has been done with several of them. Without exception it was found that these diagonal vessels connect with the radiating branches of the umbilical artery, and the latter was followed right up to its entrance into the embryo. These diagonal vessels convey the embryonic blood to the inner surface of the layer of columns. Therefore, in the columnar layer, the embryonic blood runs from the boundary between the columnar and spongy parts of the placenta to the embryonic surface of the placenta. The maternal and the embryonic blood flow through very narrow, parallel vessels in opposite directions. This is in conformity with the observations of the aforementioned authors. The opposite directions, followed by the maternal and embryonic blood in the placenta, ensures that the gradient remains constant over the whole length of the vessels.

The fully established placenta of *Elephantulus* during the later part of pregnancy consists of two parts, designated as the spongy layer and the

columnar layer. These two parts are clearly demarcated from each other. Whereas the maternal blood percolates through the whole placenta, the foetal circulation is restricted to the columnar layer only. Also structurally the two parts are vastly different from each other, as their names imply. In the columnar layer the maternal and foetal blood run in straight vessels, all parallel to each other and at right angles to the foetal surface of the placenta. In the spongy layer the blood-spaces, filled with maternal blood only, follow an irregular course and thus give to this part a spongy appearance, although, on the whole, the blood flows from the foetal side to the attached peduncle of the placenta, thus going in a peripheral direction. Further, the histological structure of the walls of the maternal blood-spaces offers a noteworthy difference when the columnar and spongy parts of the placenta are compared (fig. 49). In both parts these walls are of trophoblastic origin. In the columnar layer the wall is very thin, thus facilitating the exchange between the maternal and embryonic blood. In the spongy part the wall is thick. The columnar layer is a collection of blood-vessels, parallel to each other and separated by as little tissue as possible. In the spongy layer the tissue preponderates, and the maternal blood circulates through that tissue.

During the development the spongy layer is the first to appear, and it has already reached a considerable size before the columnar layer develops. This spongy layer is formed by the trophoblastic ectoderm only; it is, therefore, a typical ectoplacenta. When in the 18-somites stage the allantois touches the placenta, it soon spreads out over the whole inner surface of the placenta; this is achieved when the embryo has 27 somites. The contact with the allantois heralds a new phase of activity in the placenta, and an enormous multiplication of the nuclei in the zone directly facing the allantois sets in; this zone has been called the proliferative zone. This proliferation results in the formation of the columnar layer, as an entirely new structure, towards the embryonic side. Here tissue of trophoblastic origin alternates with the capillaries growing out from the allantoic vessels; the trophoblastic tissue forms narrow vessels conveying the maternal blood. On the other hand, the original placenta, now the spongy layer, is not fundamentally changed, and the allantoic vessels will never penetrate into it. It receives many new nuclei from the proliferative zone, and its formerly cellular structure is replaced by a syncytium; the trabeculae become increasingly narrower and the blood-spaces between them more numerous, but it retains the same spongy appearance which it already had before the allantois made contact with the original placenta. The proliferative zone becomes less pronounced later, and by the time the columnar layer is fully established it has disappeared altogether, being again incorporated into the spongy layer.

The following points need particular emphasis:—

(1) The placenta has already reached a considerable size before the allantois establishes contact with it.
(2) This original placenta remains as the spongy layer till the end of pregnancy, and forms at least half of the volume of the fully established placenta.
(3) The maternal blood flows first through the columnar layer and then percolates through the spongy layer.
(4) The embryonic blood never enters the spongy layer.

These facts indicate that the placenta has a dual function. The exchange of food and waste material between the mother and the embryo can only be performed in the columnar layer. It has been suggested that in the spongy layer, or at least in such parts of the mammalian placenta into which the embryonic vessels do not penetrate, food is given off by the maternal blood to the embryonic tissue, and such food is handed over from cell to cell until it finally reaches the allantoic vessels. In view of the structure of the placenta of *Elephantulus* such a suggestion has to be ruled out. The spongy layer can only be regarded as a gland with internal secretion, formed by the embryo and discharging its products into the maternal blood to influence the mother for the benefit of the embryo.

Elephantulus, with its sharp and striking division of the placenta into a columnar and a spongy part, in which, moreover, the direction of the circulation of the maternal as well as of the embryonic blood could be ascertained without doubt, proves to be a most favourable animal for the study of the structure of the placenta, and this structure is so clear that it gives a trustworthy indication of the function. Provided with this knowledge, an attempt can now be made at a survey of other mammals in this respect.

In several other mammals a similar division of the placenta into two parts has been described.

The nearest approach to the arrangement, met with in *Elephantulus*, is found in the hedgehog. According to Resink (1903), the placenta of *Erinaceus* is characterised by the formation of a dense felt of allantoic vessels and elongated trophoblastic lacunae. It is separated from the ectoplacenta by a stratified layer, which by active proliferation provides the material for the felt-like layer. In later stages the stratified layer becomes less defined. This is all in correspondence with the findings in *Elephantulus*; the felt-like layer evidently corresponding to the columnar layer. In the South African hedgehog a columnar layer is as well developed as in *Elephantulus*. At the uterine side it is covered by a spongy layer or ectoplacenta which, however, in the stage available for study with an

embryo of 19 mm., is only very thin. The whole placenta is separated from the decidua by a thick fibrous layer.

In the golden mole, *Eremitalpa granti*, the two layers of the placenta are also present, but the plane separating them is very irregular, and, therefore, the division of the placenta into two parts is not so obvious as in *Elephantulus* or *Erinaceus*.

Ericulus, according to Strauss (1943), has a central, euplacental layer and a peripheral ectoplacenta, and the capillaries in the euplacenta are vertically arranged. His figures also show that the placenta of *Ericulus* has a columnar and a spongy layer.

In *Hemicentetes* Goetz (1937 *b*) found the outer part of the placenta formed by a syncytial system of lacunae, consisting of foetal tissue, but containing only maternal blood. Towards the inside there is a system of wider lacunae with embryonic capillaries between the lacunae. So in *Hemicentetes* a similar division of the placenta exists as in *Elephantulus* and *Ericulus*, although the part corresponding to the columnar layer is spongy in appearance. It is therefore the more surprising that the direction of the maternal blood-flow should be opposite to that of *Elephantulus* and *Ericulus* (see p. 553).

On the other hand, in *Sorex*, according to Hubrecht (1893), the allantois, with the embryonic blood-vessels, penetrates through the whole thickness of the placenta, so there is nothing left that can be compared with the spongy layer of *Elephantulus*.

Bats are remarkable in this respect. Nolf (1895) says that in *Vespertilio* the allantoic villi penetrate through the whole thickness of the placenta; but, according to Branca (1927), the embryonic circulation never reaches the external surface of the placenta. De Lange (1933) mentions that in *Miniopterus* (Kempermann) there is a main placenta and two additional placentas. The main placenta is like that of *Vespertilio*, with maternal and foetal blood. The additional placentas, however, are like the early one in *Vespertilio* and, like the ripe placenta of the Rhinolophidae, have only a small amount of foetal blood but much maternal blood.

Also according to de Lange (1933), the ripe placenta of *Galeopithecus* is partly a labyrinth and partly a placenta olliformis, but he does not say if there is foetal blood in the labyrinth.

Turner (1873) found that in the sloths the foetal capillary network extends throughout the whole thickness of the placenta.

On the other hand, in *Procavia* (Sturgess, 1948) the foetal capillaries are found in the inner half of the zonary placenta only, whereas the peripheral layer consists of a lacunar system filled with maternal blood. Assheton (1906) found the same in the elephant; the inner layer here consists of branched foetal vessels and maternal blood surrounded by a syncytium,

whereas the outer layer is formed by branched trophoblastic lacunae filled with maternal blood.

It appears from Hill's (1932) description that the Primates are very interesting in this respect.

In *Tarsius* the early placenta consists of a syncytial network, derived from the trophoblast, and the lacunae are filled with maternal blood. It is an ectoplacenta, differing in no other way from the early placenta of *Elephantulus* than that the latter is cellular and the former, according to Hill, is formed by a syncytium. At a later stage in *Elephantulus* also the cell membranes disappear, and the spongy part of the placenta becomes syncytial. When in *Tarsius* the allantois comes into contact with this ectoplacenta, mesodermal villi, carrying embryonic capillaries, start to penetrate the ectoplacenta. At least that is what Hill says. However, his fig. 44 so closely corresponds to what can be observed in *Elephantulus*, that it is more likely that ectoplacental villi, carrying maternal blood, grow out into the mesoderm of the allantois, leaving the ectoplacenta itself as it was before. In either case, by this ingrowth or outgrowth, a new layer of the placenta is formed, consisting of interdigitating chorionic and allantoic villi, with the result that now the placenta consists of a columnar layer and a spongy part. Hill's figs. 45 and 46, illustrating the young placenta of *Tarsius*, differ only from a corresponding stage of *Elephantulus* by the more coarse interdigitating villi of the columnar layer. Otherwise there is the same clear-cut separation of the two parts of the placenta. It appears, however, that in *Tarsius* the mesodermal villi at a later stage penetrate deeper into the substance of the ectoplacenta, branching and subdividing at the same time. But between these villi the spongy ectoplacental tissue remains, as shown in Hill's fig. 47. The spongy and columnar parts of the placenta then become mixed up, and they can be recognised only with difficulty.

In a *Chrysothrix*, with an embryo of 6·8 mm., the mesodermal villi penetrate through the whole thickness of the placenta. Between them are large intervillous spaces, formed by a syncytial network and lacunae filled with maternal blood. This intervillous network takes no active part in the formation of the mature placenta, but structurally, in Hill's figures, it has the appearance of the spongy layer in *Elephantulus*. According to Hill, the primary functions of the early trophoblastic proliferation, which later forms the intervillous syncytium, are (1) to effect the implantation of the blastocyst into the endometrium, and (2) to provide a thick spongy, syncytial bed, vascularised by maternal blood, into which the chorionic villi can grow and branch, so as to bring the foetal blood into the closest possible relation with the maternal. Once those functions have been achieved, its usefulness is over and it undergoes degeneration. In later stages, when the embryo is 25 mm. long, the intervillous syncytium is greatly reduced. In

general, the Platyrrhine placenta undergoes its greatest growth in what are relatively late foetal stages; and, says Hill, it is an interesting fact that during this period also it attains its maximum grade of functional efficiency, so far as may be judged from its structural condition. In older embryos the syncytium is more and more reduced, and more or less completely converted into "fibrinoid" masses, presenting a laminated, fibrous and amorphous appearance. But a peripheral syncytium is still present at the outer surface of the placenta. In the nearly ripe placenta the villi are profusely branched and form a network surrounded by maternal blood, but the syncytial network has practically disappeared, only occasional masses and layers of fibrinoid tissue being present, and the peripheral syncytium is greatly reduced. The primary trophoblastic proliferation, forming the syncytial network, is far more massive in the Platyrrhines, and persists for a longer period, than in the Catarrhines. In the latter the implantation syncytium seems to be all that is left of the spongy layer.

It can be seen, therefore, that the syncytial spongy mass, filled with maternal blood, and in no close contact with the embryonic capillary system, becomes more and more reduced if we advance from *Tarsius*, via the Platyrrhina, to the Catarrhina, and also that this reduction takes place during the development of the individual placenta. This spongy, syncytial mass corresponds, in my opinion, to the spongy layer of the *Elephantulus* placenta. In *Elephantulus* this layer persists throughout pregnancy as an integral part of the placenta, and its structure gives clear evidence that it is a physiologically active organ up to the time of parturition.

Summarising this review of the literature, it can be stated that in several mammals with a haemo-chorial placenta, two parts in this placenta can be recognised. The allantoic vessels, filled with embryonic blood, penetrate into one of these parts only, whereas the maternal blood circulates through the whole placenta. The second part, therefore, contains maternal blood only. In some of these mammals the direction of the maternal circulation is known with certainty, and it appears that in all these, except *Centetes* according to Goetz, the maternal blood, on entering the placenta, first circulates in that part where the embryonic vessels are found. It is only here that an exchange of material in both directions between the maternal and embryonic blood can take place. Before leaving the placenta the maternal blood percolates through another part of the placenta, where there is no embryonic blood. In none of these mammals is the division of the placenta into two parts so clear as in *Elephantulus*, yet it does exist. In some, particularly in the Primates, the division is clear only at an earlier period of pregnancy and becomes progressively obscured later on. Finally, no division of the placenta into two parts may be discernible from the beginning of its formation.

The structure of the placenta of *Elephantulus* clearly shows that the products of the spongy part can only be discharged into the maternal blood. Without coming into close contact with the embryonic blood, they are directly transported by the placental vein and distributed by the maternal circulation. The contention was made that the spongy part of the placenta constitutes a gland with internal secretion, formed by the embryo and discharging its products into the maternal blood to influence the mother for the benefit of the embryo. The presence of a similar part in the placenta of several other mammals, with a haemo-chorial placenta, has been demonstrated. It follows that the placenta of these mammals has a similar function.

Not in all mammals with a haemo-chorial placenta, however, can such a glandular part be indicated with the same clearness as in *Elephantulus*. This does not mean that it is absent. It is well known to gynaecologists that the human placenta secretes hormones, such as gonadotrophin and progesterone. Also, recent studies indicate that the gonadotrophin is produced by the cytotrophoblast, and the steroid hormones, which include progesterone, by the syncytial trophoblast. The spongy part of the placenta of *Elephantulus* is a derivative of the trophoblast only; the allantoic mesoderm never penetrates into it, nor does any other tissue, except, of course, the maternal blood circulating through the channels. The trophoblast layer in the columnar part of the placenta of *Elephantulus*, where the exchange between the maternal and embryonic blood takes place, is exceedingly delicate. When comparing with this layer the trophoblast layer of the human placenta, it is at once obvious that the latter is a very thick and robust epithelium. Moreover, Fujimura (1921) showed that this epithelium has a secretory function. It is, therefore, likely that this epithelium, not only concerning its origin but also in respect of its function, corresponds to the spongy part of the *Elephantulus* placenta. The trophoblast layer of the human placenta becomes much thinner in the second half of pregnancy and then assumes the character of an endothelium, whereas the spongy part of the placenta of *Elephantulus* probably retains its secretory function till parturition; but this does not obviate this contention. It is, for example, well known that the corpora lutea remain active throughout pregnancy in some mammals, and become redundant and degenerate during the later part of pregnancy in other mammals; yet they are homologous structures.

Whether a similar relation between mother and embryo exists in mammals, other than those with a haemo-chorial placenta, is difficult to say. A careful study of both the morphological and the physiological aspects of their placentation may reveal this.

Some Important Moments in the Embryonic Life of Elephantulus.

It appears that there are two moments during the embryological development of *Elephantulus* that are of particular importance; they can be regarded as real turning-points in the life of the embryo. A third moment is, of course, that of birth at the end of gestation, but this is beyond the scope of the present study.

The first important moment in the embryonic life is when the early embryo arrives at the implantation site; this really is the beginning of gestation. The uterus is prepared for the reception of the embryo, and the embryo is ready to continue its development. Yet it is only when the embryo arrives at the implantation site that an interaction between the uterus and the embryo can be observed, on the one hand, enabling the embryo to proceed with its further growth and differentiation, and on the other hand, stimulating the uterus to inaugurate a complex series of reactions, necessary for the accommodation and the sustenance of the embryo.

The second event of major importance in the life of the embryo occurs at about mid-term, or maybe slightly later. The embryo is then about 5 mm. long. At that moment several changes take place simultaneously in the uterus and the embryo, demonstrating that a turning-point is reached. In the embryo the anterior somites become unrecognisable and the formation of the organs is initiated. The allantois has completely surrounded the yolk-sac, which results in a fundamental change in the method of nutrition. A rudiment of the secondary placenta appears, which may be related to this change in nutrition and, although this placenta is of a very temporary nature only, its formation is certainly a noteworthy event. According to Gilbert (1944) the mesonephroi do not make their appearance until the embryo is larger than 4 mm., but they are already highly developed at the time the embryo is 6 mm. long. In the uterus the decidual reaction has reached the limits of its extension in the decidua spongiosa; the decidua compacta is completely destroyed. The decidua pseudocapsularis is forced open, giving the embryonic membranes access to the main uterine cavity. The hitherto active growth of the uterine wall at the mesometrial side is succeeded by a more passive stretching of the antimesometrial wall, resulting in a change of the conceptus from a hemispherical to a spherical form.

Not every organ is affected by this sudden change in the life of the embryo. Notably the elaboration of the columnar layer of the placenta, which starts when the embryo has developed 18 somites and comes to an end only when the embryo is about 18 mm. long, proceeds unimpeded.

Up to this moment the growth of the embryo is very slow; after four

weeks of pregnancy it has reached a length of about 4 mm. only. From now on the embryo may grow more vigorously, although there are no reliable indications of a more rapid growth.

Next in importance is the moment when the embryo reaches a length of 18 mm. It is unknown whether at that time any major changes in the embryo itself occur. What happens is that the decidua compacta and spongiosa are now completely destroyed, that the decidual arteries are straightened out to short and wide channels; the narrow constriction in the artery where it leaves the muscularis has disappeared, so that the maternal blood can flow without hindrance to the placenta. The placental circulation thus is stabilised, and the placenta itself has reached its definitive structure, as shown by the disappearance of the layer of proliferation. These changes in the placenta and its blood-supply no doubt have a profound effect on the nutrition of the embryo. The accelerated growth of the embryo is shown by the change in the form of the conceptus; up to the 18 mm. stage it was spherical, now it suddenly becomes cylindrical.

At what moment in time this change in the nutrition and growth of the embryo occurs is difficult to say. As said on p. 439, on 7th October six females were collected, three of which were in early pregnancy for the second time of the season, and the other three had embryos of 18·5, 29 and 36 mm. length. On the 14th October five animals were collected in early second pregnancy, and a sixth had an embryo of 28·6 mm. These few data give at least an indication that the change, taking place at the 18 mm. stage, occurs rather late during the gestation period, and thus that the growth after this moment is very vigorous.

Besides these major turning-points in the life of the embryo, other events, equally decisive for the well-being of the embryo, can be recognised. But they are not so sudden in their appearance; they show a more gradual development. Most conspicuous amongst these is the elaboration of the columnar layer of the placenta, which results in a complete change in the feeding mechanism of the embryo. The formation of this layer, however, starts already, when the embryo has only 18 somites; it continues to develop unimpeded during the eventful period when the embryo is about 5 mm. long, and finally it ends when the embryo is 18 mm. long. During all this long time the haemo-chorial allantoic placenta gradually gains in importance as the major organ for the nutrition of the embryo, but there is at no time a sudden change in its function. Only at the end, as mentioned above, such a change may occur.

In a previous publication (van der Horst and Gillman, 1946 *a*) it was shown that the corpora lutea pass through four successive stages during the course of pregnancy. It seemed worth while to investigate whether there is any relation between these stages and the various changes taking place in

the uterus and the embryo. The results of this investigation proved to be rather disappointing.

Once the corpus luteum has assumed its spherical form and is embedded in the substance of the ovary, which has been achieved when the early blastula has arrived at the implantation site, it steadily grows until the embryo is about 10 mm. long. During all this period the corpus luteum does not show any change in the structure of its cells, and it may be assumed, therefore, that also no change in function takes place. Yet during this period the most important change in the embryonic life can be observed when the embryo is 5 mm. long.

When the embryo is 10 mm. long the corpus luteum stops its growth, and it will retain the same volume until the embryo is about 20 mm. long. During this stage a single, large vacuole appears in each individual cell and disappears again. So there is a remarkable change in the corpus luteum when the embryo is ten mm. long, but no corresponding change has been observed in the embryo or uterus. Only the embryonic erythrocytes begin to lose their nuclei when the embryo has reached a length of 10 mm.; this process ends when the embryo is 15 mm. long. It is doubtful whether there is any direct relation between the loss of these nuclei and the occurrence of the large vacuoles in the yellow cells. Both processes begin at the same time, but the one ends long before the other.

When the embryo is about 20 mm. long the corpora lutea suddenly begin to increase in volume again, caused by an extension of each individual cell, and this increase continues until the embryo is approximately 30 mm. long. This sudden growth indicates a renewed activity of the corpora lutea. It has been pointed out above that a major change in the embryonic life occurs when the embryo is about 18 mm. long. In this instance a close relation between the two events is at least possible. The difference in size of the embryos, of 18 and 20 mm. is small, and probably is of no significance in this respect.

The data concerning the existence or non-existence of some relation between consecutive stages in the evolution of the corpora lutea and the changes taking place in the embryo and uterus are few in number, even in *Elephantulus*, of which a large amount of material was available for study. Even so it is worth mentioning them, as such a relation might be anticipated. It is well known that the behaviour of the corpora lutea of the different mammals shows a great amount of variation. A great diversity also exists in the course of embryonic development. Only a careful study of several species of mammals may yield satisfactory and reliable results.

SUMMARY.

In the previous pages the various constituent parts of the uterus, the placenta and the embryonic membranes of *Elephantulus*, and their metamorphoses during the course of pregnancy, have been discussed and compared with the corresponding structures in other mammals. This comparison made it possible to arrive at certain conclusions respecting the morphology of the various organs. Only the structure, as revealed in serial sections, was studied, but as structure and function are intimately connected in an indivisible whole, it is often possible to draw conclusions about the function from a study of the structure. Moreover, the ever-changing structure during the course of embryological development is in itself a physiological process revealed in the structure.

The more salient results of this study can be summarised as follows:

1. In *Elephantulus* both localisation and orientation of the implantation site are determined. In other mammals the embryo may implant anywhere in the uterus, or either localisation or orientation may be determined.

2. As in the rabbit, three periods can be recognised during pregnancy in respect to the changes taking place in the uterine wall: (1) a period of preparation; (2) a period of active growth; (3) a period of passive stretching The first period begins before ovulation and ends when the embryo arrives at the implantation site. During the second period only a small segment of the uterine wall at the mesometrial side is involved; the decidual reaction is restricted to this segment, which greatly extends and soon forms at least half of the uterine wall; the result is a hemispherical swelling. When the embryo is about 5 mm. long this growth stops, and the hitherto inactive antimesometrial side of the uterine wall becomes stretched, the conceptus assumes first a spherical and, when the embryo is about 20 mm. long, a cylindrical form.

3. Upon arrival of the embryo at the implantation site, an embryo-chamber is formed here in which the embryo closely fits. This formation is a reaction of the uterine wall to the presence of the embryo. No similar embryo-chamber is known to exist in other mammals, except to some extent in man. The edge of the embryo-chamber is comparable to the decidua capsularis in man. The decidua capsularis of *Erinaceus* is a different structure, as well as the decidua lateralis of *Sorex*.

4. In reptiles, birds and marsupials the polar differentiation of the embryo is determined by the structure of the egg. In Placentalia polarity is the result of forces acting inside the embryo. In *Elephantulus* the maternal tissues induce the polarity of the embryo.

5. In contrast to other Placentalia the period between ovulation and

implantation can be subdivided into two stages, viz. that of transportation, and that of the embryo lying free in the embryo-chamber.

6. In all Placentalia the time between fertilisation and implantation is rather constant and lasts about 7 to 9 days, irrespective of the duration of gestation. In all, except *Elephantulus*, the embryo is in the blastocyst stage when it arrives at the implantation site, and the embryo implants at once; the period of transportation is long. In *Elephantulus* this period is short, but the embryo remains free at the implantation site until it invades the mucosa in the blastocyst stage.

7. Unlike other mammals, the four-celled embryo of *Elephantulus* is dependent on the implantation site for its continued development.

8. Implantation starts with the outgrowth of finger-like processes of plasmoditrophoblast when the embryo is in the early primary amniotic cavity stage. These primary villi bear no relation to the openings of the glands.

9. As in *Talpa*, no mitotic division occurs in the plasmoditrophoblast.

10. The finger-like villi broaden out along the basement membrane of the decaying chamber epithelium, thus anchoring the embryo in the embryo-chamber.

11. Having pierced the basement membrane, the plasmoditrophoblast at once surrounds the dilated subchamber capillaries, which subsequently are opened by the cytotrophoblast.

12. The maternal tissue is destroyed by the cytotrophoblast and not by the plasmoditrophoblast.

13. The plasmoditrophoblast sends out deep roots into the healthy uterine wall. These roots serve to anchor the embryo temporarily. Similar deep roots were found in *Talpa* (Vernhout), in *Cavia* (Grosser), in *Tarsius* and monkeys (Hill).

14. The lacunae between the cytotrophoblastic villi do not connect with the maternal vessels later on, as said by Vernhout, Hubrecht and Resink. These lacunae are opened-up capillaries and filled with maternal blood from the beginning.

15. The cytotrophoblast does not penetrate deep into the mucosa; a resistant reticulum is formed by the uterus, preventing deeper penetration and giving a hold to the cytotrophoblastic villi. This fibrous layer remains till the end of pregnancy. Henceforth the placenta can only grow out into a centripetal direction, as also described in *Talpa* and *Erinaceus*.

16. The histiolytic action of the trophoblast in mammals with a haemochorial placenta is of short duration and often local in extent.

17. After the formation of the fibrous layer the deep plasmoditrophoblastic roots atrophy, and completely disappear in the late primary amniotic cavity stage.

18. The cytotrophoblast forms a spongy network, through which the maternal blood circulates. This ectoplacenta now consists of an anchoring part, enmeshed in the reticulum and a spongy part; the latter grows out into the uterine lumen.

19. During the primitive streak stage and the formation of the first 14 somites, the ectoplacenta grows out into a bell-shaped structure. Two central placental arteries pervade the whole thickness of the placenta and branch into a number of radiating vessels along the surface of the placenta facing the embryo. From these radiating vessels arises a network of channels, forming the spongy part of the placenta. Several placental veins arise near the pedunculated base of the placenta and fuse to a single decidual vein.

20. The maternal blood circulates through the ectoplacenta from the embryonic side towards the attached base of the placenta. The same direction of the blood circulation is found in several mammals with a haemochorial placenta (bats, hedgehog, *Procavia*, *Muridae*, *Ericulus*).

21. The ectoplacenta, up to the 18-somites stage, is connected to the embryo by an *a*-vascular chorion only.

22. In the early primitive streak stage *Elephantulus* has a connecting stalk like *Tarsius*; it disappears in the late primitive streak stage.

23. In the 18-somites stage the allantois has made contact with the ectoplacenta.

24. The allantois completely covers the embryonic surface of the placenta at the 27-somites stage.

25. The allantois of *Hapale*, in some respects, is intermediate between the allantois of *Elephantulus* and the connecting stalk of monkeys and man.

26. Immediately after the allantois has made contact with the ectoplacenta, a zone of intense proliferation appears along the plane of contact. From this zone numerous nuclei penetrate into the spongy ectoplacenta, which changes from a cellular structure into a syncytium but otherwise retains its form and structure until the end of pregnancy. This syncytium is a different thing from the plasmoditrophoblast. Also by this proliferation a new layer is added to the placenta towards the embryonic side. In this columnar layer the maternal blood channels are in close apposition to the allantoic vessels.

27. In contrast to many other mammals, the allantoic mesoderm, with the embryonic blood-vessels, never penetrates into the spongy ectoplacenta.

28. The placenta is stabilised and the proliferating zone has disappeared when the embryo is 18 mm. long.

29. The full-grown placenta consists of three parts; a columnar layer, a spongy part, and a very narrow anchoring layer.

30. The maternal and the embryonic blood flow in parallel vessels and in opposite directions in the columnar layer of the placenta. In a few other mammals the directions were found to be opposite.

31. The stabilised placental circulation is shown schematically in fig. 71.

32. The allantois, having spread over the inner surface of the placenta, grows down as a narrow sac along the inside of the chorion, and further between the yolk-sac and the trophoblast.

33. An extensive, although not voluminous, allantois is a primitive feature in mammals.

34. The part of the trophoblast, protruding in the main uterine lumen after the destruction of the decidua pseudocapsularis, becomes multilayered. This stratification is present only in an embryo between 5 and 8 mm. long. This stratified part of the trophoblast is a rudimentary secondary placenta the formation of which is induced by the allantois.

35. There is a close relation between amniogenesis and placentation. In *Elephantulus* and monkeys the amnion is formed by cavitation; this has no direct influence on the formation of the placenta. When the embryonic disc is exposed, as in *Sorex*, *Talpa* and *Tupaia*, the amnion is formed by folding and the placentation is influenced accordingly. Amnion formation by folding causes *Tarsius* to form a placenta corresponding to the secondary placenta of the monkey.

36. The haemo-chorial placenta of *Elephantulus* corresponds to the primary placenta, and the rudimentary placenta to the secondary placenta, of the monkey.

37. Histologically there is a great difference between the columnar layer and the spongy part; the first is an assemblage of maternal and foetal blood-vessels with thin walls, thus facilitating the exchange of food and waste material; in the spongy part the tissue preponderates and the maternal blood circulates through it.

38. The spongy layer has reached a considerable size already before there is a columnar layer, and retains this size till the end of pregnancy. The maternal blood flows first through the columnar layer and then through the spongy part. It is concluded that the spongy part of the placenta is a gland with internal secretion, formed by the embryo and discharging its product into the maternal blood to influence the mother for the benefit of the embryo.

39. The two parts found in the haemo-chorial placenta of *Elephantulus*, viz. the columnar layer and the spongy part, occur also in the placentas of several other mammals (*Erinaceus*, golden mole, *Ericulus*, bats, *Procavia*, elephant, *Tarsius*, and in monkeys during the earlier stages). The thick trophoblast layer of the human placenta may correspond to the spongy part of the *Elephantulus* placenta.

40. Mossman's definition of chorion is acceptable only if it is realised that this mammalian chorion corresponds to a part of the chorion of reptiles and birds only.

41. The yolk-sac reaches its peak of development when the embryo is in the primitive streak stage.

42. The yolk-sac becomes completely vascularised by omphaloidean vessels.

43. The entodermal yolk-sac is completely separated from the trophoblast by the allantois when the embryo is about 6 mm. long; the yolk-sac then becomes greatly reduced in size.

44. With the yolk, the yolk-ectoderm of the Sauropsida and Marsupialia has completely disappeared in the Placentalia. The yolk-sac of the Placentalia is a structure different from the yolk-sac of the Sauropsida.

45. The mammalian yolk-sac has an important function in feeding the embryo during the first part of pregnancy; it absorbs the uterine milk. This function is taken over by the allantois later on.

46. When the embryo of *Elephantulus* is about 5 mm. long, the embryonic membranes enter the main uterine cavity, forcing open the canal between the bursa embryonica and the main uterine cavity.

47. Vascularity is not a necessary attribute of a placenta. Any fusion or intimate apposition of the foetal membranes to the uterine tissues for the purpose of feeding the embryo can be considered a placenta.

48. *Elephantulus* simultaneously has a localised haemo-chorial placenta and an extensive epithelio-chorial placenta of a primitive form. Several other mammals have two types of placenta. There is no reason to compare a haemo-chorial placenta of the higher Primates or the lower Insectivores with the epithelio-chorial placenta of Lemurs, etc. The absence of a haemo-chorial placenta in the mole *Scalopus* or in the Lemurs can be explained as a sudden loss.

49. When the embryo consists of sixteen cells the glands have the form of a corkscrew; next the distal part of the glands, surrounding the embryo-chamber, starts to swell enormously.

50. In the blastocyst stage the swollen parts of the glands flatten out in tangential direction, reducing the tissue between them to narrow septa.

51. This metamorphosis of the glands differentiates the mucosa into a central decidua compacta and a peripheral decidua spongiosa.

52. At the 13-somites stage the destruction of the septa between the glands begins; this results in the formation of a continuous cavity separating the decidua from the muscularis.

53. The glandular cells, lining the inner aspect of the muscularis as an uninterrupted layer, remain vital during the rest of pregnancy.

54. At first only the glands related to the embryo-chamber react, later

on those in the lateral walls begin to swell, whereas the glands in the antimesometrial part of the uterus do not show any reaction.

55. By the swelling of the glands the lateral walls of the uterus bulge out into the lumen, and in this way a decidua pseudocapsularis is formed, separating a bursa embryonica from the main uterine lumen.

56. The decidua pseudocapsularis is destroyed when the embryo is 5 mm. long.

57. The glands provide all necessary food during the first four weeks of pregnancy. During this time growth in bulk of the embryo is slow. The transition from nutrition by glandular secretion to that by the haemochorial placenta is gradual. In the following four weeks growth becomes more vigorous and the embryo increases in size from 4 mm. to 4 cm.

58. The anterior somites start to grow out when the embryo is four weeks old and 4 mm. long.

59. The oestrus oedema is distributed over the whole endometrium; the nuclei and the vacuoles are much larger than during anoestrus, and there is intense mitotic activity.

60. After ovulation the stroma gets a dense appearance through the great number of nuclei and the small vacuoles.

61. The oestrus oedema is not an indication that the uterus is ready to receive the embryo. Only in the dense stroma stage, following ovulation, the uterus is prepared for the reception of the embryo.

62. The pregnancy oedema, formed after the arrival of the embryo at the implantation site, is restricted to the mesometrial wall of the uterus.

63. The localised pregnancy oedema is different in nature from the general oestrus oedema.

64. The decidual reaction is restricted to the mesometrial side of the uterus. This originally very small part of the uterine wall greatly expands during the first period of pregnancy.

65. A real decidual reaction does not take place in the decidua lateralis and the decidua pseudocapsularis.

66. In the early blastocyst stage the decidual cells assume a pear-shape. Starting from around the embryo-chamber, this reaction gradually spreads towards the muscularis. The early giant cells appear.

67. The decidual reaction is already well advanced when the embryo grows out its primary villi.

68. In the late primitive streak stage the number of large giant cells in the decidua compacta has reached its peak; the pear-shaped cells have disappeared, some by transformation into giant cells, others by changing into highly vacuolated cells with conspicuous cell walls.

69. When the embryo has 13 somites, many giant cells in the decidua compacta are broken down; they enter the decidual arteries, and can be

found as emboli in the spongy part of the placenta. This seems to be the case also in *Tarsius*.

70. Giant cells are destroyed in the central part at the same rate, as they are formed more towards the periphery.

71. The breaking down of the decidua compacta is already well under way when the embryo has 18 somites; the decidua spongiosa then is not yet fully differentiated.

72. Giant cells penetrate into the lumen of the decidual arteries and form a new, very thick wall; the arterial lumen may be completely blocked up.

73. When the embryo is about 5 mm. long, the decidua compacta is completely destroyed and the decidual reaction has reached its limit in the decidua spongiosa.

74. In some mammals (rabbit, *Orycteropus*, *Sorex*) giant cells are of embryonic origin, in *Elephantulus* they are maternal.

75. The giant cells of *Elephantulus* are glandular in nature. Their product is removed by the maternal blood, but has to pass the ectoplacenta first. It is not likely that the product feeds the embryo.

76. After the total destruction of the decidua, including the glands, the embryo and placenta are lying free in the enlarged uterine cavity, suspended to the muscularis by the decidual arteries and vein only.

77. The decidual arteries and veins become conspicuous as swollen vessels in the blastocyst stage, but exist before that time.

78. The decidual arteries, at first, are swollen in the peripheral part of the decidua compacta and to a less extent in the decidua spongiosa. The connection with the arteries in the muscularis remains very narrow. The arteries follow an extremely meandering course in the decidua, far more so than in any other mammal. In the central part of the decidua compacta they become straight and narrow, to widen again as a network of swollen capillaries directly surrounding the embryo-chamber. The capillaries are opened up by the invading cytotrophoblast.

79. In contrast to other mammals, *Elephantulus* has three coiled arteries only.

80. The decidual arteries have no side branches.

81. In their distribution the decidual arteries are sharply restricted to the decidua compacta and spongiosa; the rest of the uterine wall is supplied by other branching arteries.

82. When the embryo has about 35 somites and the uterine swelling measures 10×6 mm., the coiled artery is approximately 9 cm. long. The decidua compacta is then already destroyed and the artery is here straightened out; but for this the artery might have been 20 cm. long.

83. Two of the three coiled arteries fuse to form one placental artery, the third continues as the second placental artery.

84. There is only one decidual vein, which has the character of an ordinary vein.

85. The destruction of the decidua compacta and spongiosa is accompanied by a great shortening of the decidual arteries; when the destruction is complete, these arteries are reduced to straight, but wide, vessels about 2 mm. long. The narrow connection with the myometrial artery also becomes wide. The embryo is then about 18 mm. long.

86. Except for *Choloepus*, coiled arteries are only known to exist in the lower Insectivores (*Centetes*, *Elephantulus* and *Erinaceus*) and in the higher Primates. In the Platyrrhines they are present in a simple, straight form.

87. The coiled decidual arteries are different in form and function from the spiral arteries found in the ovary.

88. Unlike the Centetidae, and maybe other mammals, the coiled arteries of *Elephantulus* are completely destroyed during pregnancy and newly formed after parturition.

89. The difference between the oestrus oedema and the pregnancy oedema may be related to the existence of two kinds of arteries in the mucosa, ordinary arteries and coiled arteries. Only the coiled arteries are affected by progesterone.

90. The embryo of *Elephantulus* can implant in a very restricted area only; this may be explained by the fact that all three coiled arteries end at this place.

91. There is no shifting of the implantation site at subsequent pregnancies.

92. There seems to be a relation between the occurrence of menstruation and the presence of coiled arteries in mammals.

93. Changes of major importance take place in the development of the embryo when it arrives at the implantation site, and again when the embryo is about 5 and about 18 mm. long.

94. No relation could be established between the consecutive stages in the appearance of the corpora lutea and these changes in the life of the embryo, with the possible exception at the time the embryo is 18 mm. long.

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[TEXT-FIGS. 1–71.

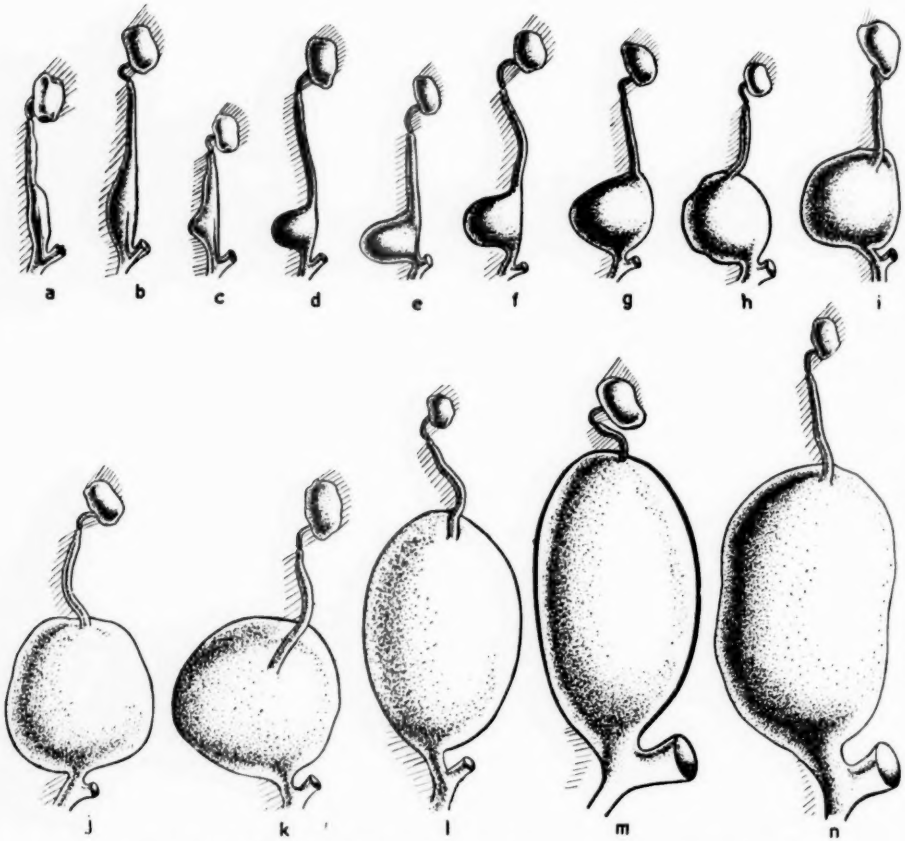


FIG. 1.—The right uterine horn and ovary during the succeeding stages of pregnancy; the left horn, when necessary, was used for ascertaining the stage of development of the embryo. $\times 1\frac{1}{2}$. *a*, of a parous animal coming into oestrus; *b*, at the time of ovulation; *c*, embryo in the blastocyst stage, before implantation; *d*, late primary amniotic cavity stage; *e*, late primitive streak stage; *f*, embryo with 13 somites; *g*, embryo with 36 somites; *h*, embryo 7·4 mm. long; *i*, 10 mm.; *j*, 15·6 mm.; *k*, 19 mm.; *l*, 24·5 mm.; *m*, 30 mm.; *n*, 35 mm. Note that the conceptus is hemispherical up to *g*, then it becomes spherical, and from *l* onwards elongated. Also note that the originally large cranial part of the uterine horn remains unaffected during pregnancy.

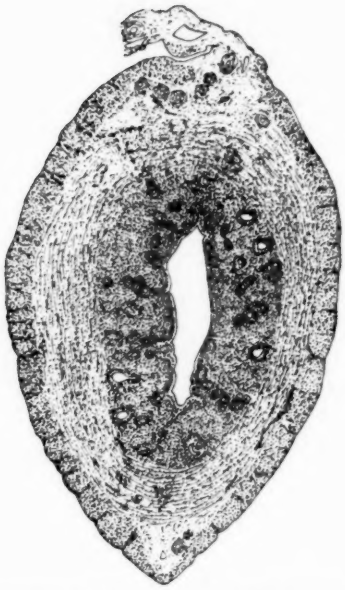


FIG. 2.—A cross-section of the uterus near the implantation site of a parous animal during anoestrus. ×40. Series 122.

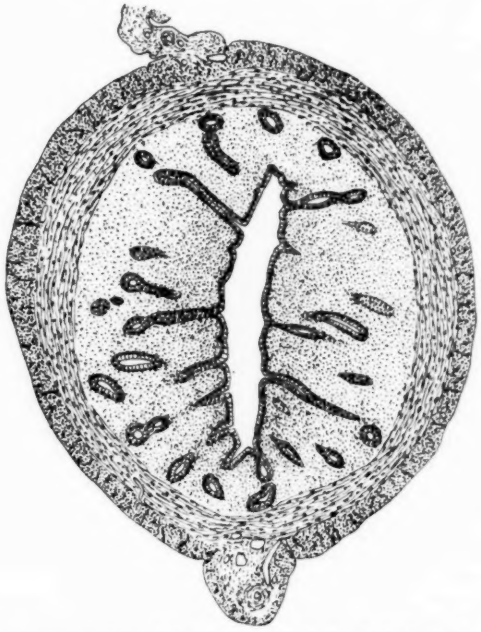


FIG. 3.—A cross-section of the uterus near the implantation site of a young animal at the time of ovulation. Note the oedematous stroma and the conspicuous, straight glands. ×40. Series 95.

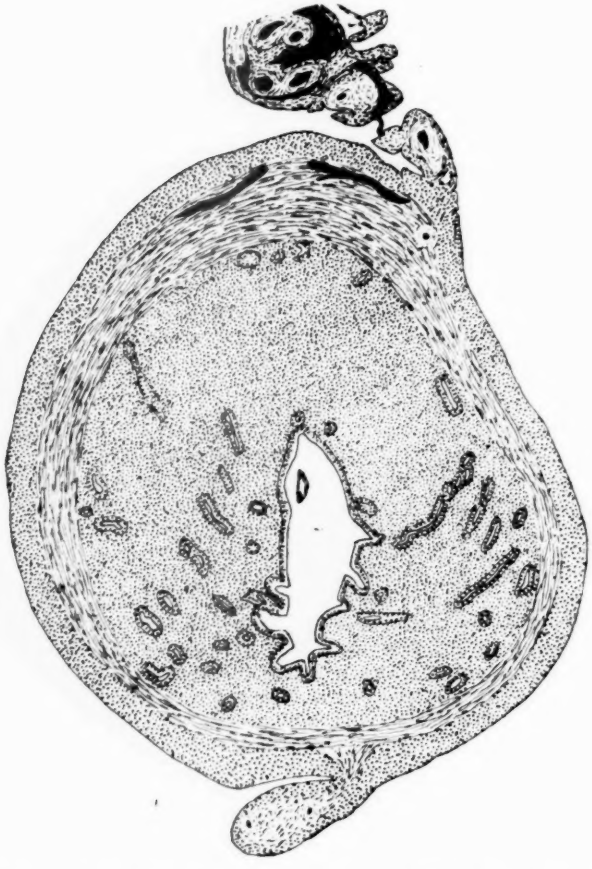


FIG. 4.—A cross-section of the uterus with a 4-celled embryo just arriving at the implantation site. Note the density of the nuclei in the stroma. ×40. Series 385.

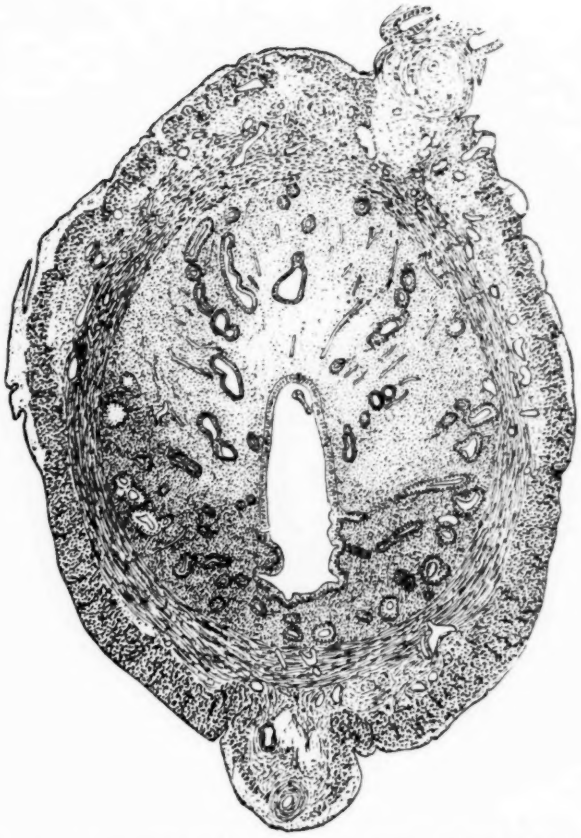


FIG. 5.—A cross-section of the uterus with an 8-celled embryo; the embryo-chamber is in the process of formation. Note the pregnancy oedema surrounding the embryo-chamber and the dark stroma at the antimesometrial side of the uterus. The glands related to the chamber begin to swell. ×40. Series 168.

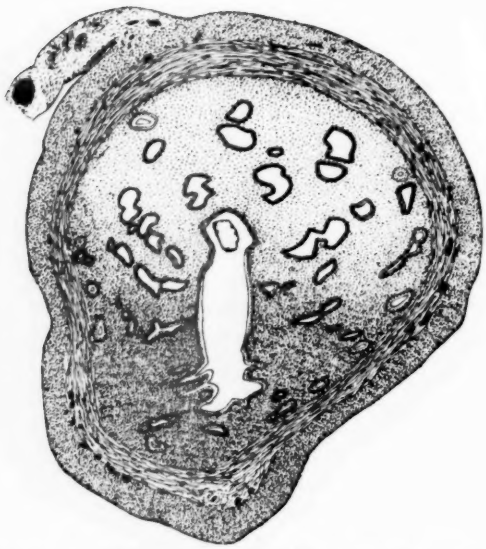


FIG. 6.—A cross-section of the uterus with a 32-celled embryo; the embryo-chamber is well formed; its wall consists of a single layer of cells. The pregnancy oedema has spread over the whole thickness of the endomebrium. The glands continue swelling and begin to take the form of a spiral. ×40. Series 824.

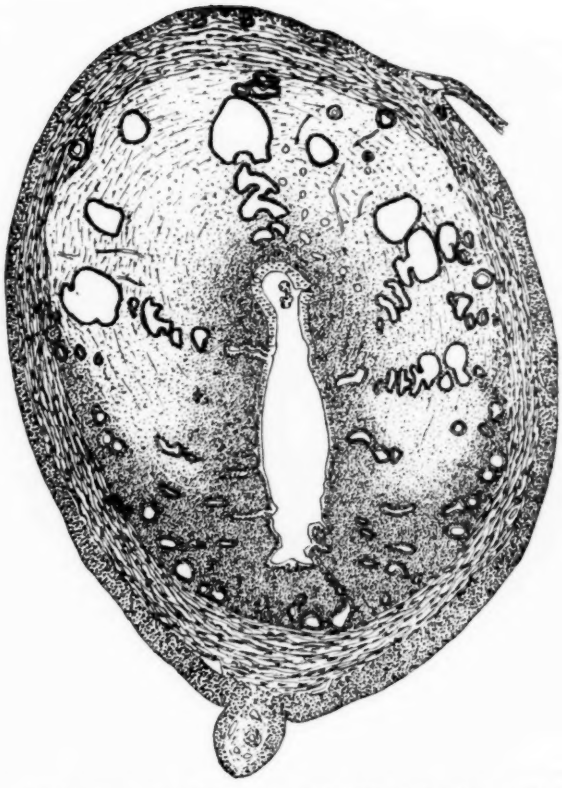


FIG. 7.—A cross-section of the uterus with a 32-celled embryo; the uterine reaction is slightly more advanced that in fig. 6. The wall of the embryo-chamber is multilayered; the decidual reaction has started round the embryo-chamber; the glands show a greatly swollen and a spiral part. ×40. Series 201.

FIG. 8.—A longitudinal section of the other horn of the same uterus as that shown in fig. 7. ×40. Series 198.

FIG. 9.—A cross-section of a uterus with an embryo in the early blastocyst stage. The embryo-chamber is clearly delimited from the main uterine cavity by a constriction; the decidual reaction has extended; the glands become flatter in a tangential direction. Note that the mesometrium is attached to the lateral side of the uterus. ×30. Series 36.

FIG. 10.—A cross-section of a uterus with an embryo in the early primary amniotic cavity stage. Implantation has started and the embryo-chamber opens up. The decidual blood-vessels have become very conspicuous; the deeper parts of the glands are greatly flattened and converge below the embryo towards the main uterine lumen. ×30. Series 222.

FIG. 11.—A cross-section of a uterus with an embryo in the primary amniotic cavity stage. The yolk-sac enlarges in the main uterine lumen. × 25. Series 486.

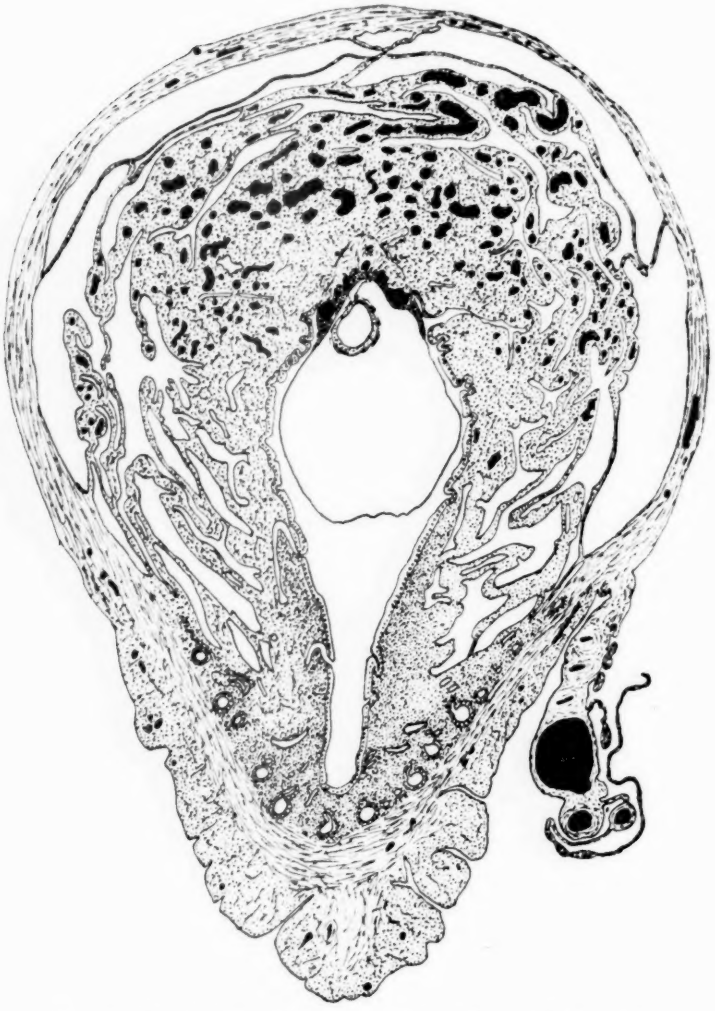


FIG. 12.—A cross-section of a uterus with an embryo in the late primary amniotic cavity stage. Note the thin septa between the greatly enlarged deeper parts of the glands. ×25. Series 760.

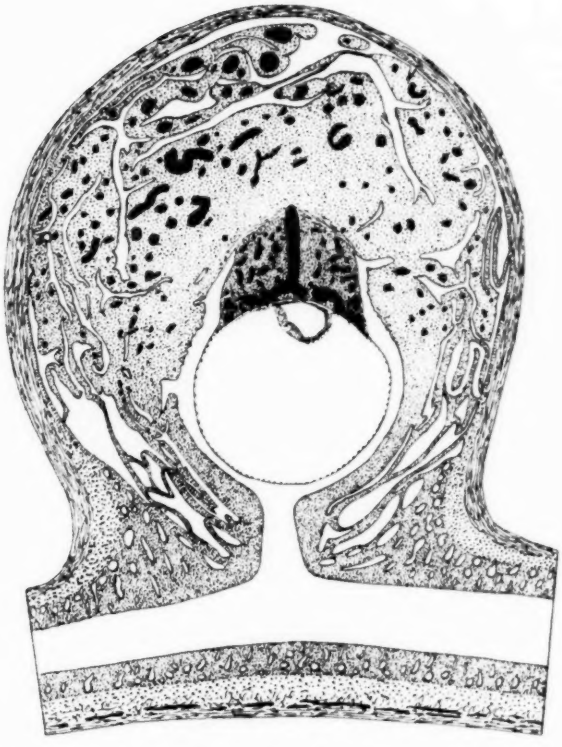


FIG. 13.—A longitudinal section of a uterus with an embryo in the early primitive streak stage, composed from a few sections. The bursa embryonica becomes constricted off from the main uterine cavity. The young ectoplacenta hangs down in the bursa. ×20. Series 780.

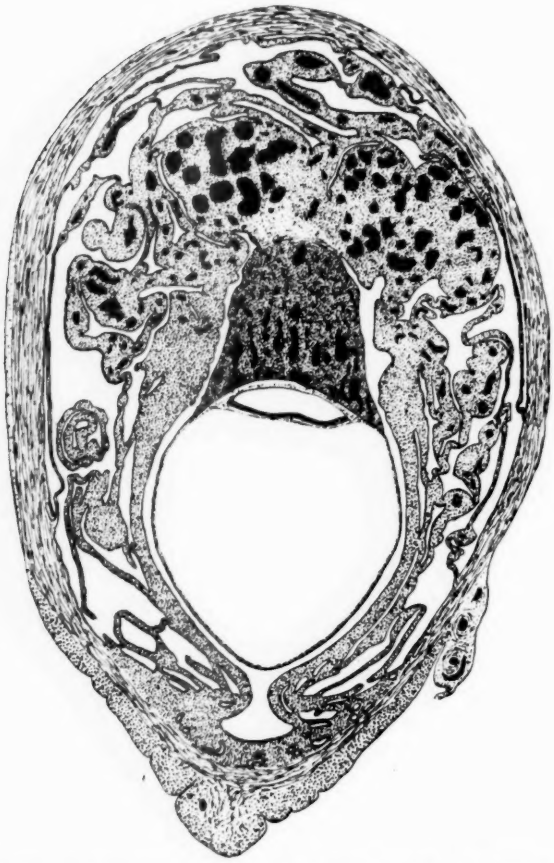


FIG. 14.—A cross-section of a uterus with an embryo in the primitive streak stage; the section is in front of the primitive streak. The bursa embryonica becomes constricted off from the narrow main uterine cavity by the decidua pseudocapsularis. ×20. Series 834.

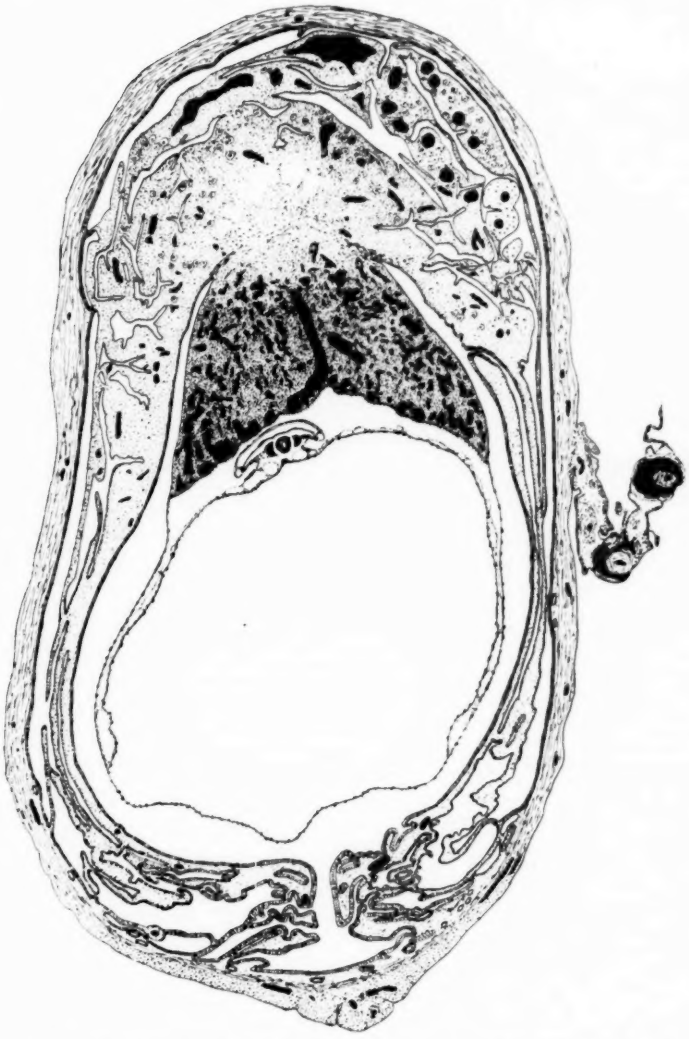


FIG. 15.—A cross-section of a uterus with an embryo with 13 somites. The bursa embryonica is well formed. The breaking down of the decidua compacta has started; the giant cells are conspicuous in the decidua spongiosa. Note one of the main placental arteries in the centre of the placenta and a part of the second artery. ×20. Series 833.

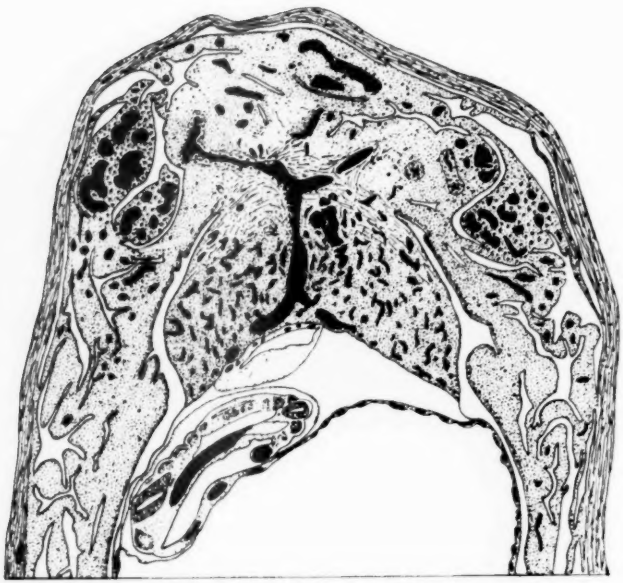


FIG. 16.—The mesometrial half of a cross-section of a uterus with an embryo with 22 somites. The central part of the decidua compacta is already destroyed. The as yet small allantois is pressed against the ectoplacenta. Note the fusion of two decidual arteries to one placental artery; that at the embryonic side of the placenta again splits up into radial vessels. ×20. Series 788.

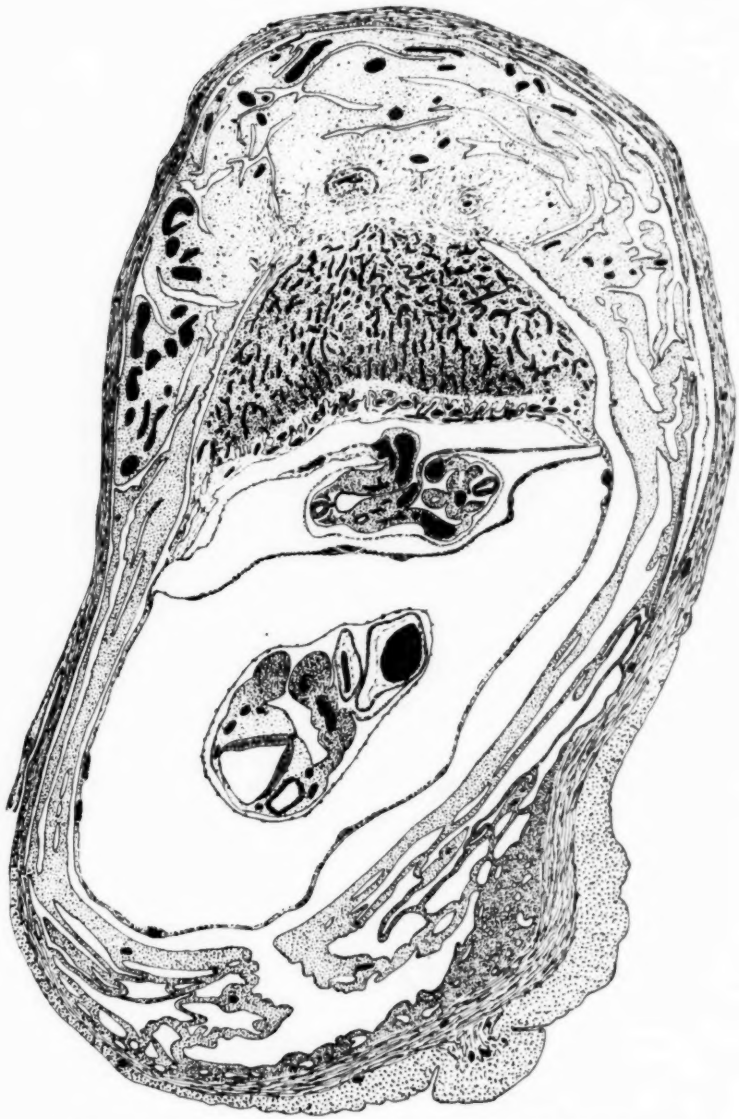


FIG. 17.—A cross-section of a uterus with an embryo with 27 somites. The septa between the glands are destroyed. The allantois covers the whole embryonic surface of the placenta and the formation of the allantoic placenta has started. Note the zone of proliferation, characterised by the density of nuclei, in the placenta. The head of the embryo, dipped in the yolk-sac, is surrounded by the pro-amnion. The mesoderm has completely surrounded the yolk-sac. ×20. Series 866.

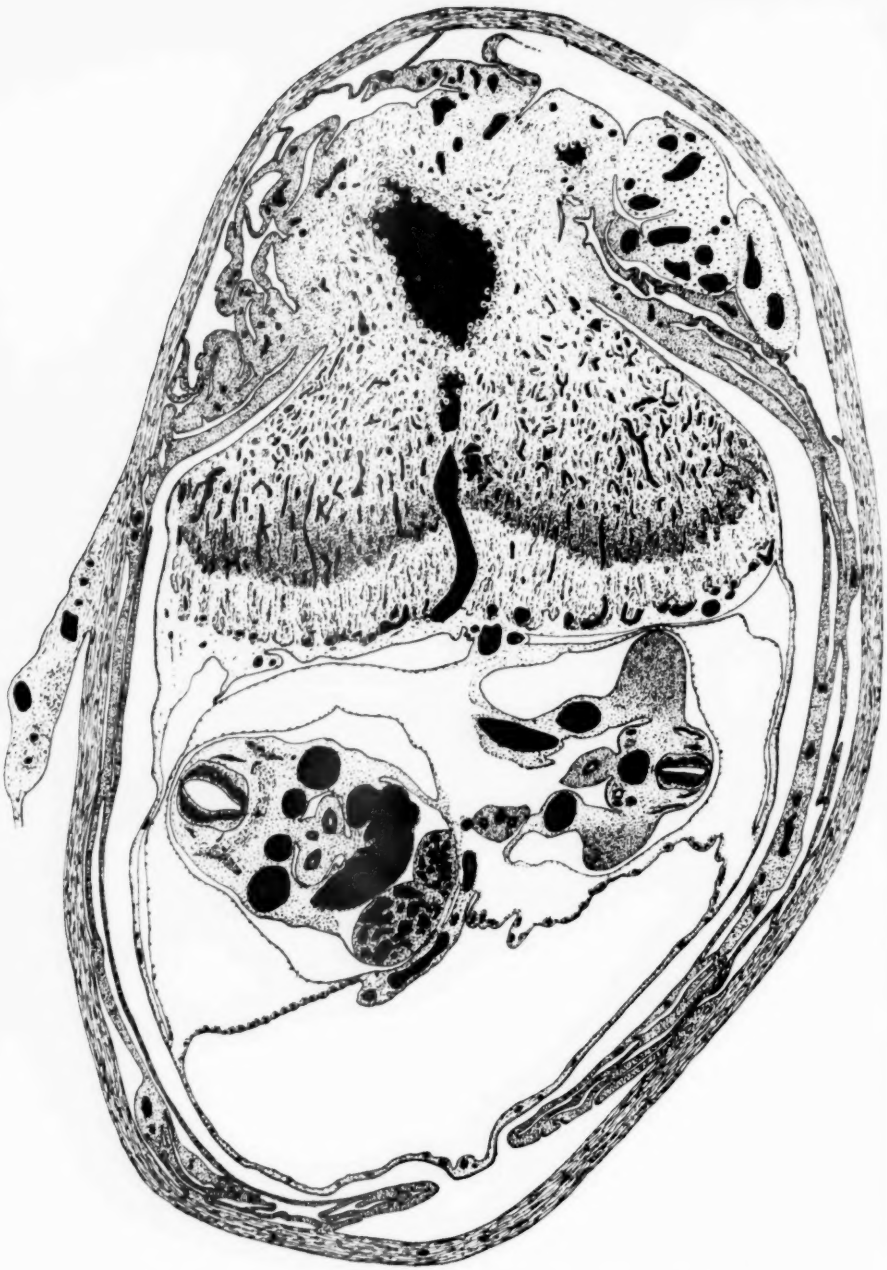


FIG. 18.—A cross-section of a uterus with an embryo 4·9 mm. long. The yolk-sac protrudes into the main uterine cavity; the decidua pseudocapsularis is in reduction. The allantois forms a narrow cavity surrounding the exocoelom. The allantoic placenta is separated from the ectoplacenta by the zone of proliferation. ×20. Series 801.

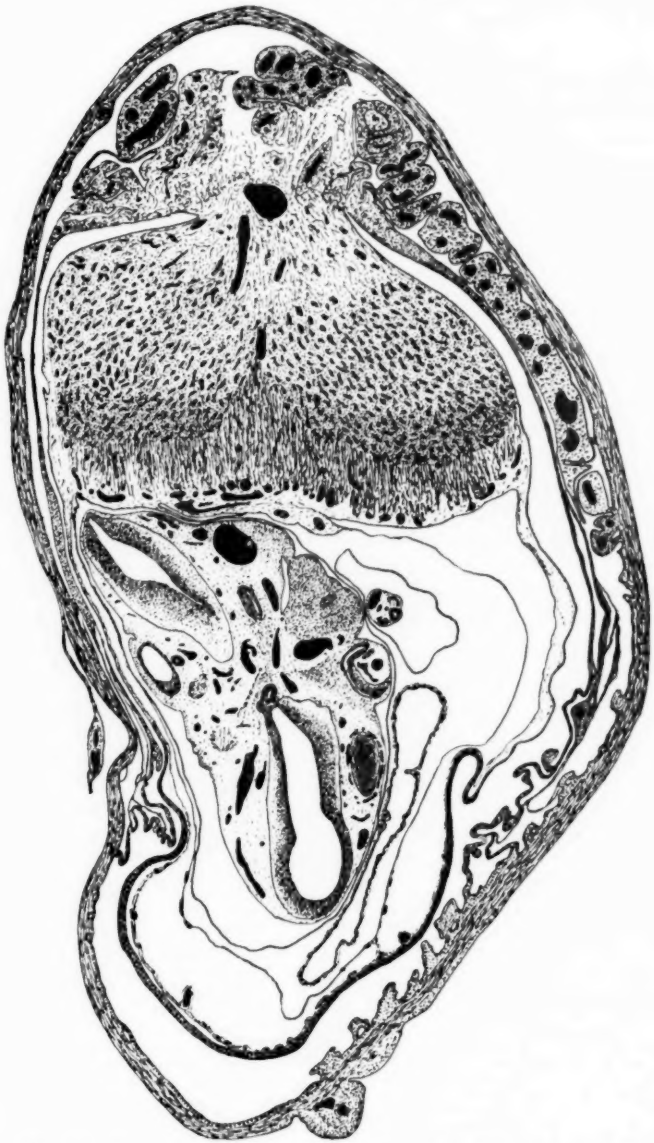


FIG. 19.—Cross-section of a uterus with an embryo 6·14 mm. long. The yolk-sac, with a thick wall, is greatly reduced in size and completely surrounded by the exocoelom and the allantois. The decidua spongiosa is partly destroyed. Only rests of the decidua pseudocapsularis are left. Note the thick chorionic ectoderm where the embryonic membranes extend into the distended main uterine cavity. × 15. Series 567.

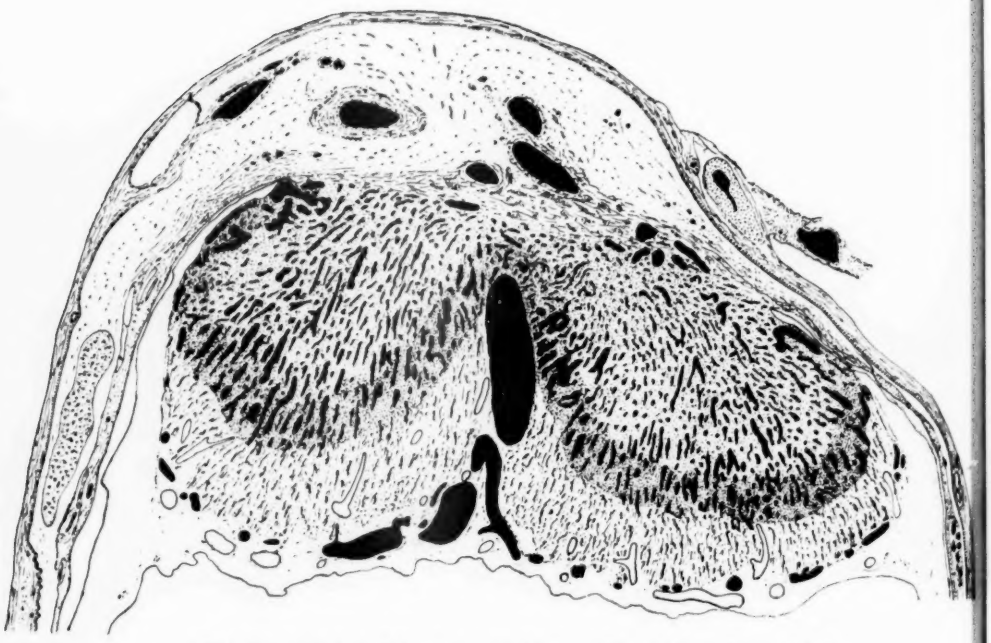


FIG. 20.—A section of the placenta and surrounding uterine wall, associated with an embryo 10 mm. long. Only a small portion of the decidua spongiosa, to the left in the figure, remains. The zone of proliferation is still conspicuous in the placenta. The allantoic vessels in the columnar part of the placenta are open, the maternal blood is black. ×20. Series 464.

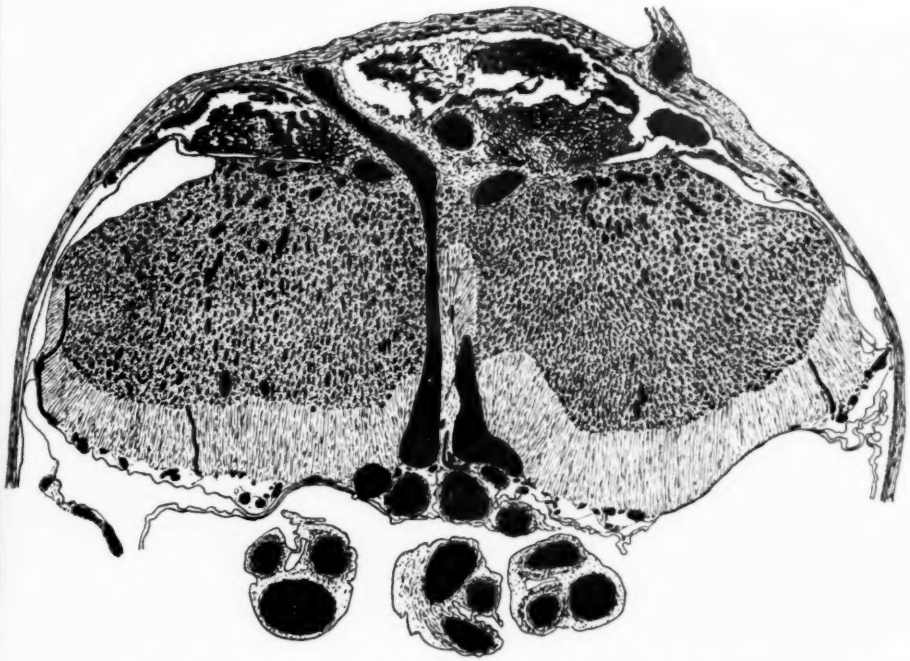


FIG. 21.—A section of the placenta associated with an embryo 38 mm. long. Note the short, straight decidual artery, continued into one of the central placental arteries. The zone of proliferation between the columnar and spongy parts of the placenta has disappeared completely. Three diagonal arteries can be seen crossing through the columnar layer. Note the position of the mesometrium near the axis of the placenta. ×15. Series 820.

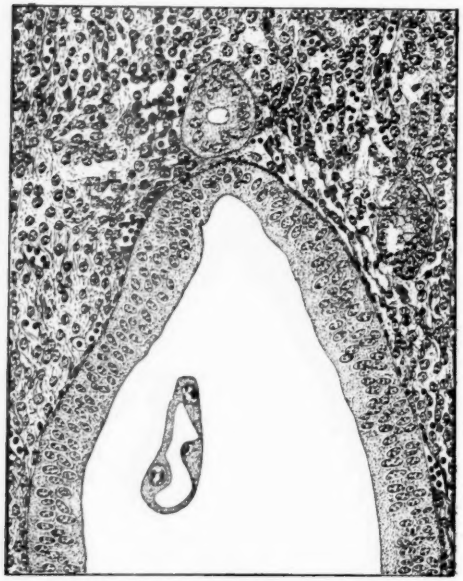


FIG. 22.—Part of the same cross-section shown in fig. 4. There is as yet no embryo-chamber and the stroma is dense. A gland is about to open in the uterine lumen. ×200. Series 385.

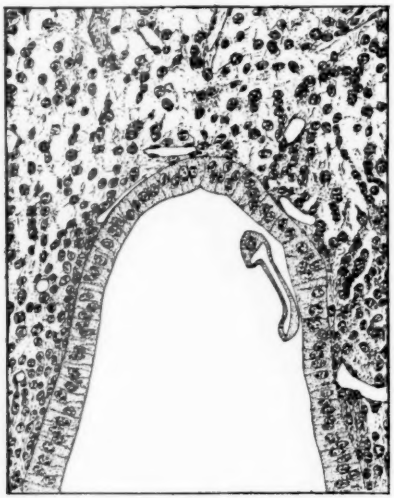


FIG. 23.—Part of the same cross-section shown in fig. 5. The embryo-chamber is in course of formation. The stroma is oedematous. Capillaries can be seen surrounding the chamber. ×200. Series 168.

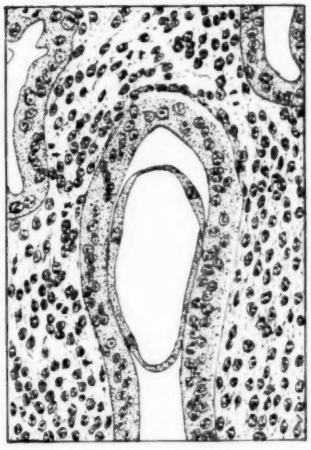


FIG. 24.—A 40-celled blastula in the embryo-chamber. ×200. Series 862.

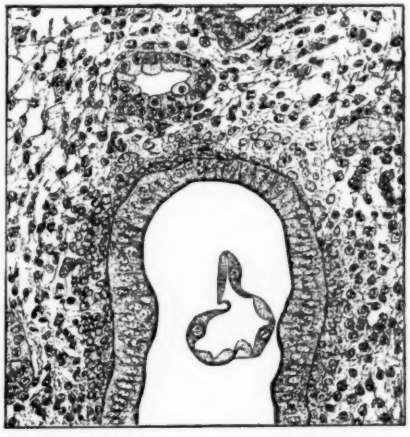


FIG. 25.—A 16-celled blastula in a well-formed embryo-chamber. ×200. Series 187.

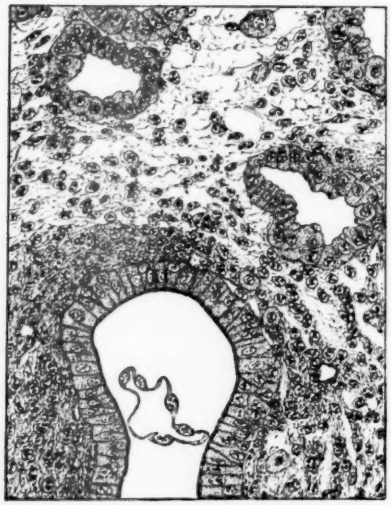


FIG. 26.—A 32-celled blastula in the embryo-chamber. The decidual reaction has started underneath the chamber epithelium. ×200. Series 58.

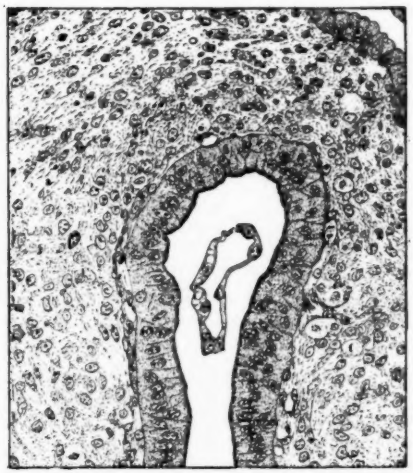


FIG. 27.—A late blastula in the embryo-chamber. The chamber epithelium has become stratified. ×200. Series 49.

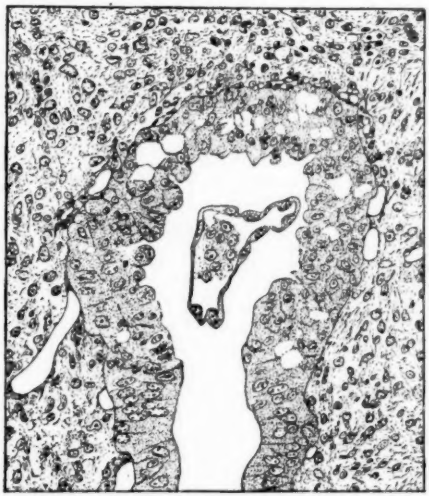


FIG. 28.—An early blastocyst in the embryo chamber. The many vacuoles are a symptom of the decay of the chamber wall. ×200. Series 62.

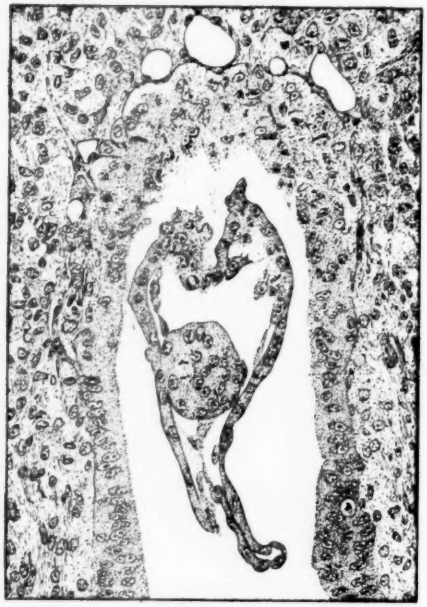


FIG. 29.—Late blastocyst in the embryo-chamber. The villi begin to grow out from the trophoblast. The capillaries surrounding the chamber are swollen. ×200. Series 35.

FIG. 30.—Two blastocysts in the embryo-chamber; only the lower one forms a yolk-sac. The destruction of the chamber epithelium is well advanced. ×200. Series 218.

FIG. 31.—An embryo in the early primary amniotic cavity stage in the embryo-chamber. The trophoblast has differentiated into a thick placental cap with two primary villi and the thin yolk-sac ectoderm. Note the healthy uterine epithelium in contrast to the decaying wall of the embryo-chamber. × 150. Series 769.

FIG. 32.—An embryo in the early primary amniotic cavity stage. The villi have penetrated the chamber epithelium and broaden out along the basement membrane. × 150. Series 52.

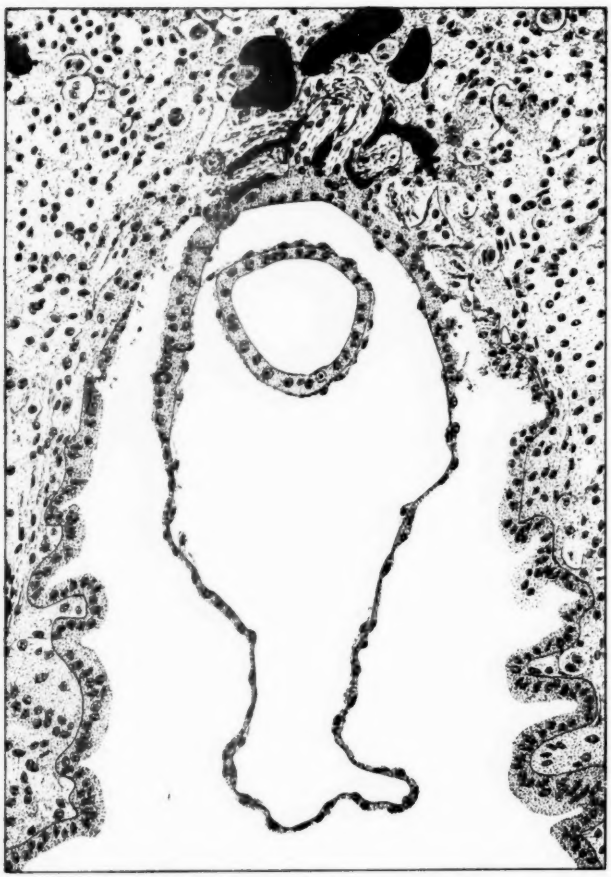


FIG. 33.—An embryo in the primary amniotic cavity stage. The chamber epithelium is completely destroyed. The villi of plasmoditrophoblast have pierced the basement membrane and surround the swollen capillaries. ×150. Series 33.

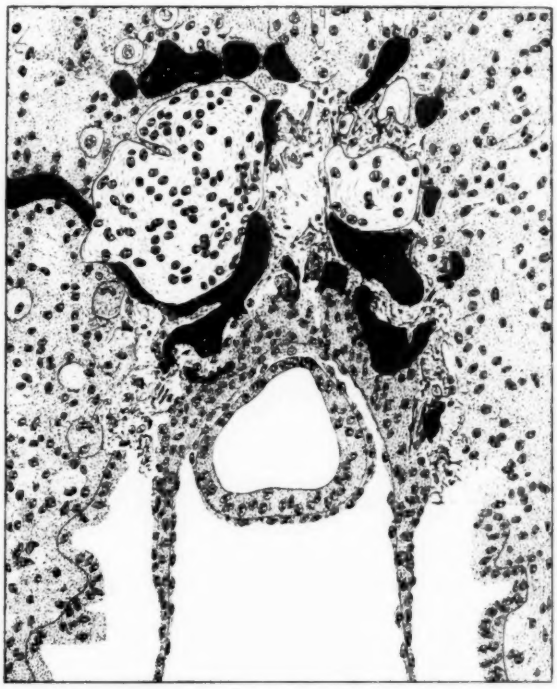


FIG. 34.—An embryo in the late primary amniotic cavity stage. Large masses of plasmoditrophoblast surround the swollen capillaries. The cytotrophoblast comes in contact with the capillaries. × 150. Series 65.

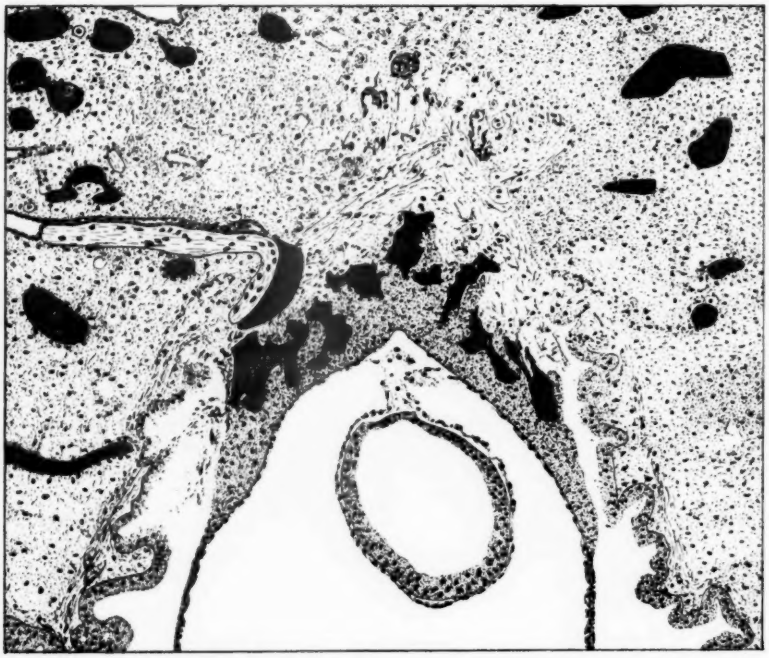


FIG. 35.—An embryo in the late primary amniotic cavity stage. The cyto-trophoblast has opened the capillaries. To the left a deep root of plasmodi-trophoblast penetrates into the stroma alongside a gland. ×100. Series 69.

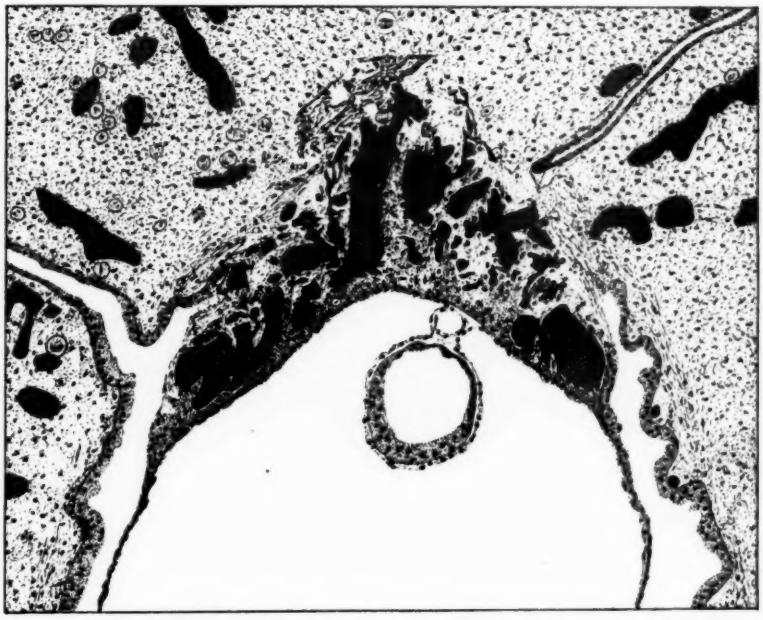


FIG. 36.—Embryo in the late primary amniotic cavity stage. Early placenta; the two placental arteries can be recognised in the centre. × 100. Series 767.

FIG. 37.—Embryo in the primitive streak stage. The ectoplacenta is clearly separated from the endometrium by a felt-like tissue. Note the central placental arteries. ×100. Series 530.

FIG. 38.—Embryo with 21 somites. The allantois in the process of spreading out over the surface of the ectoplacenta. ×50. Series 790.

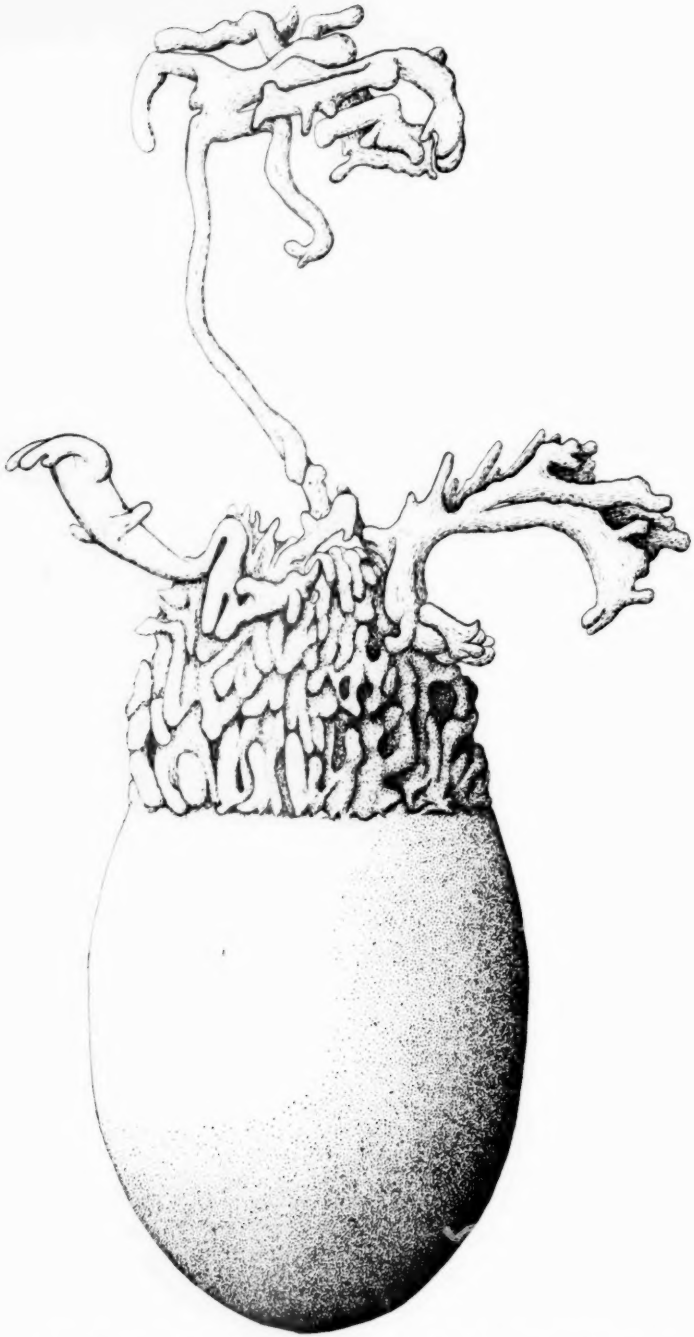


FIG. 39.—A wax-reconstruction of an embryo in the primary amniotic cavity stage. Note the placental cap and the deep roots of the plasmoditrophoblast. ×120. After series 768.

FIG. 40.—A section of an embryo in the late primary amniotic cavity stage with the deep roots of the plasmoditrophoblast in reconstruction. ×120. Series 486.

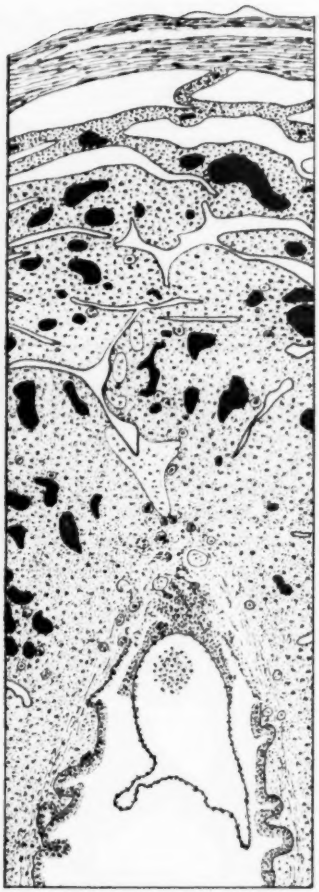


FIG. 41.—Part of a section of the uterus with an embryo in the primary amniotic cavity stage showing the depth to which the roots of plasmoditrophoblast penetrate into the uterine wall. ×50. Series 762.

FIG. 42. Part of a section of the uterine wall containing the same deep root as shown in fig. 40, bifurcating where it comes into contact with a gland, and at the other side connected to the cytotrophoblast between swollen capillaries. The uterine stroma is not affected by the deep root. ×200. Series 486.

FIG. 43.—A deep root of the plasmoditrophoblast in the course of destruction. Note the small, pycnotic nuclei. ×200. Series 70.

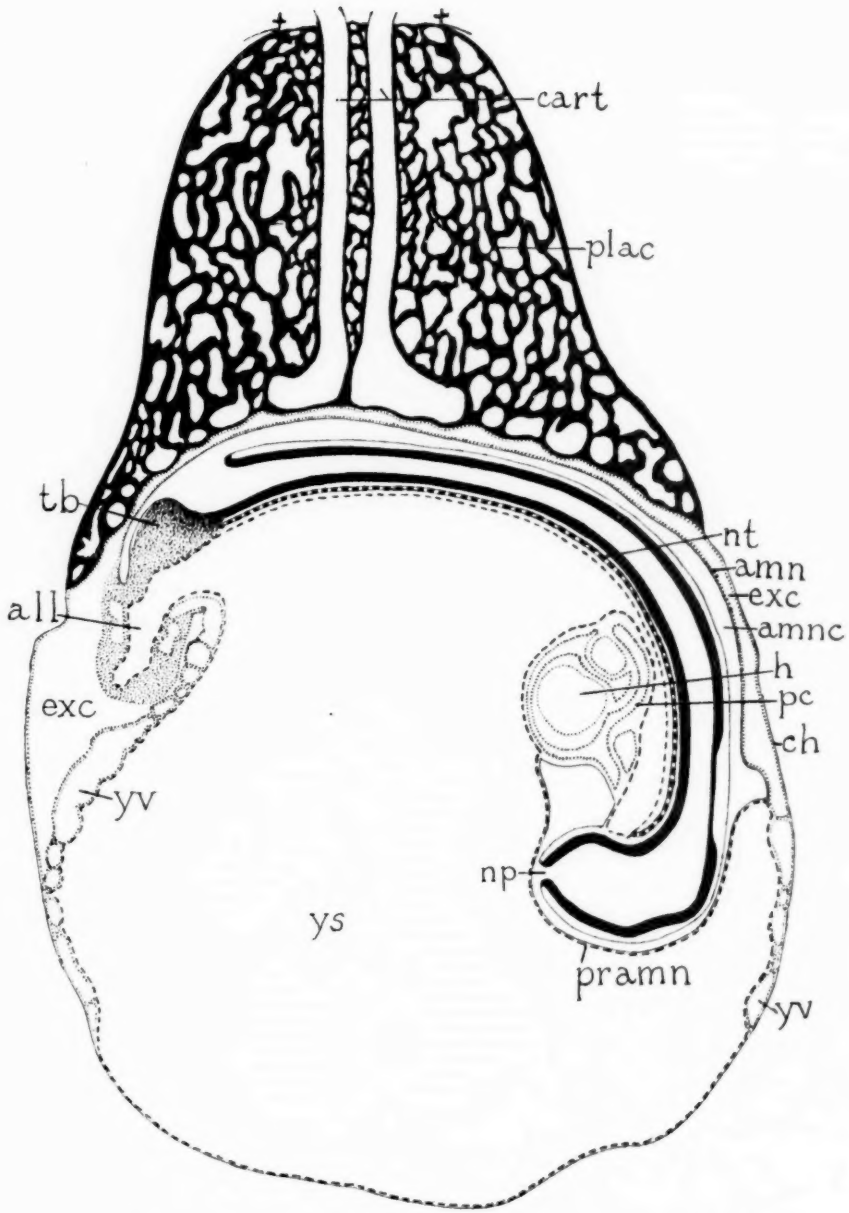


FIG. 44.—Longitudinal section of an embryo with 14 somites, composed of a few sections: *all*, allantois; *amn*, amnion; *amnc*, amniotic cavity; *cart*, the two central placental arteries; *ch*, chorion; *exc*, exocoelom; *h*, heart; *np*, neuropore; *nt*, notochord; *pc*, pericardium; *plac*, ectoplacenta; *pramn*, pro-amnion; *ys*, yolk-sac; *yv*, vitelline vessels. ×40. Series 763.

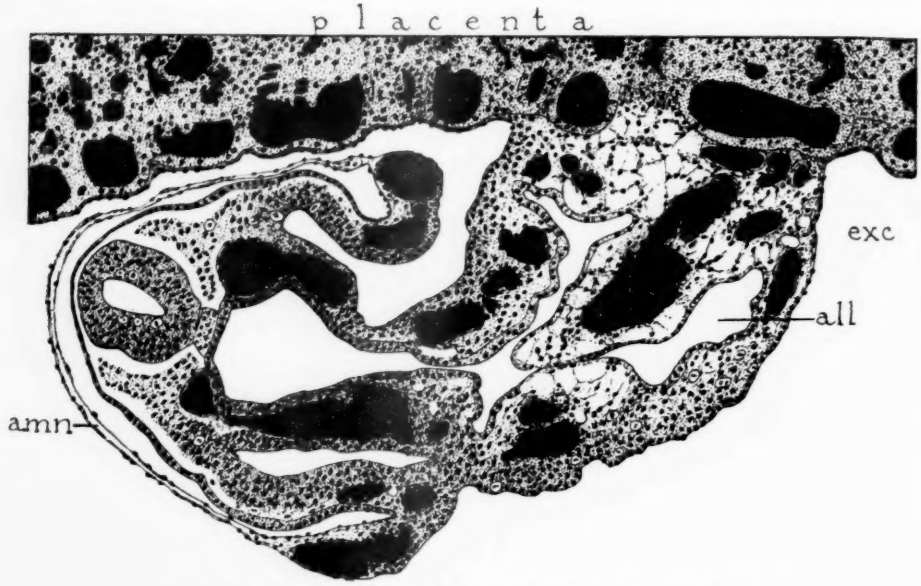


FIG. 45.—Embryo with 18 somites; the allantois making contact with the ectoplacenta: *all*, allantoic cavity; *amn*, amnion; *exc*, exocoelom. ×100. Series 754.

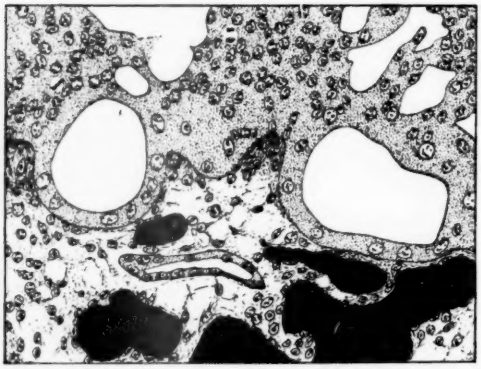


FIG. 46.—Embryo with 18 somites. The allantois, with blood-vessels in black, insinuating itself between the radial vessels of the ectoplacenta filled with maternal blood. ×200. Series 754.

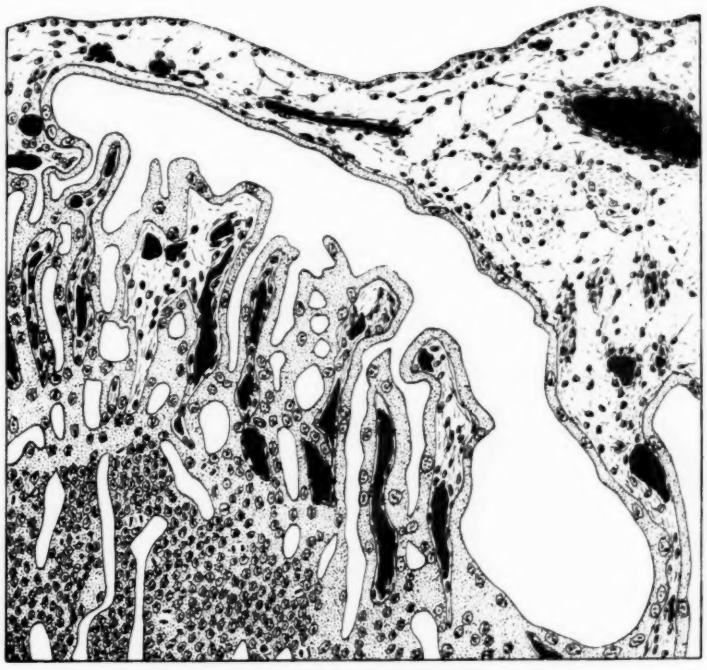


FIG. 47.—Part of a section of the placenta associated with an embryo with 34 somites. It shows the allantois with its loose mesodermal tissue, covered by a thin layer of entoderm, and the embryonic blood-vessels in black. From a central placental artery, to the right, arises a wide radial vessel. This in turn gives off several narrow branches that, together with the black embryonic vessels, first form the columnar layer and then proceed, at left bottom only, into the proliferating layer. Note the many mitotic figures in this layer. × 150. Series 771.

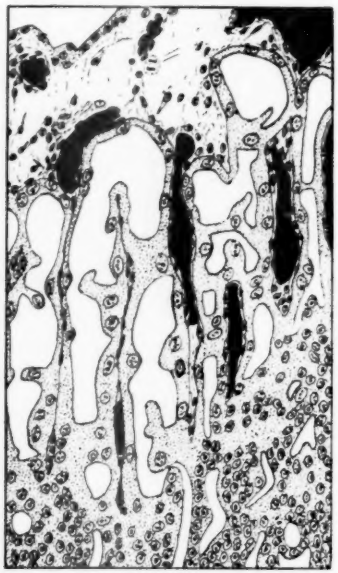


FIG. 48.—Part of a section of the columnar layer of a placenta associated with an embryo with 30 somites. The allantoic vessels are in black, the spaces filled with maternal blood are left open. ×150. Series 772.

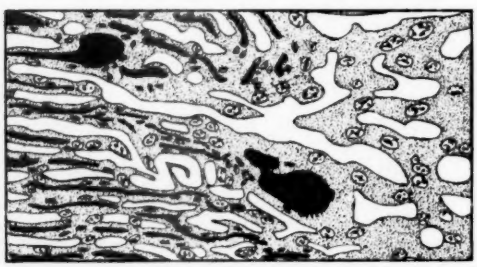


FIG. 49.—Part of a section of the placenta associated with an embryo 25 mm. long. The columnar layer with the embryonic blood-vessels in black, and the channels filled with maternal blood left open, is to the left. A collecting embryonic vein is seen near the centre. To the right is the spongy part of the placenta with maternal blood only. ×200. Series 821.

FIG. 50.—Two segments of the wall of the yolk-sac of the embryo, with 13 somites, shown in fig. 15: (*a*) lateral wall, consisting of entoderm, mesoderm with blood-vessels, and trophoblast; (*b*) obplacental wall, consisting of entoderm and trophoblast. ×200. Series 833.

FIG. 51.—Two segments of the membranes of the embryo, 4·9 mm. long, shown in fig. 18: (*a*) the lateral side, consisting of allantoic entoderm, very delicate, and mesoderm and the trophoblast; (*b*) the obplacental wall of the trilaminar yolk-sac, consisting of entoderm, mesoderm and trophoblast. ×200. Series 801.

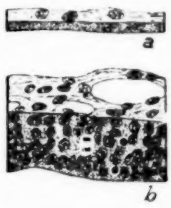


FIG. 52.—Two segments of the membranes of an embryo, 5·47 mm. long: (*a*) the lateral side, consisting of allantoic mesoderm and a thin layer of trophoblast; (*b*) the obplacental wall in the main uterine cavity, consisting of allantoic mesoderm and a thick, multilayered trophoblast (*cf.* fig. 19). ×200. Series 876.

FIG. 53.—Two segments of the membranes of an embryo, 8·16 mm. long: (*a*) the lateral side, and (*b*) the obplacental wall, both consisting of allantoic mesoderm and a single-layered trophoblast. ×200. Series 1059.

FIG. 54.—A uterine gland during anoestrus. ×150. Series 711.

FIG. 55.—A uterine gland of a full-grown but virgin animal. ×150. Series 562.

FIG. 56.—A uterine gland at the time of oestrus. ×75. Series 488.

FIG. 57.—A uterine gland associated with an embryo in the early blastula stage, showing the beginning of the spiral form. ×75. Series 60.

FIG. 58.—A uterine gland associated with an embryo in the late blastula stage, showing the unaltered fundus, the swollen part, the spiral part, and the short neck opening into the embryo-chamber. ×75. Series 98.

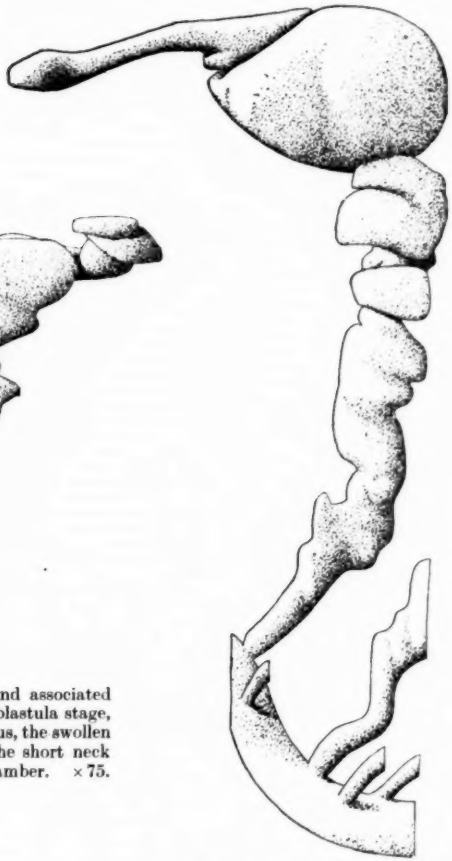


FIG. 59.—A uterine gland associated with an embryo in the early blastocyst stage, showing the fundus, the ballooned segment, the spiral, and the lengthening straight neck. ×75. Series 50.

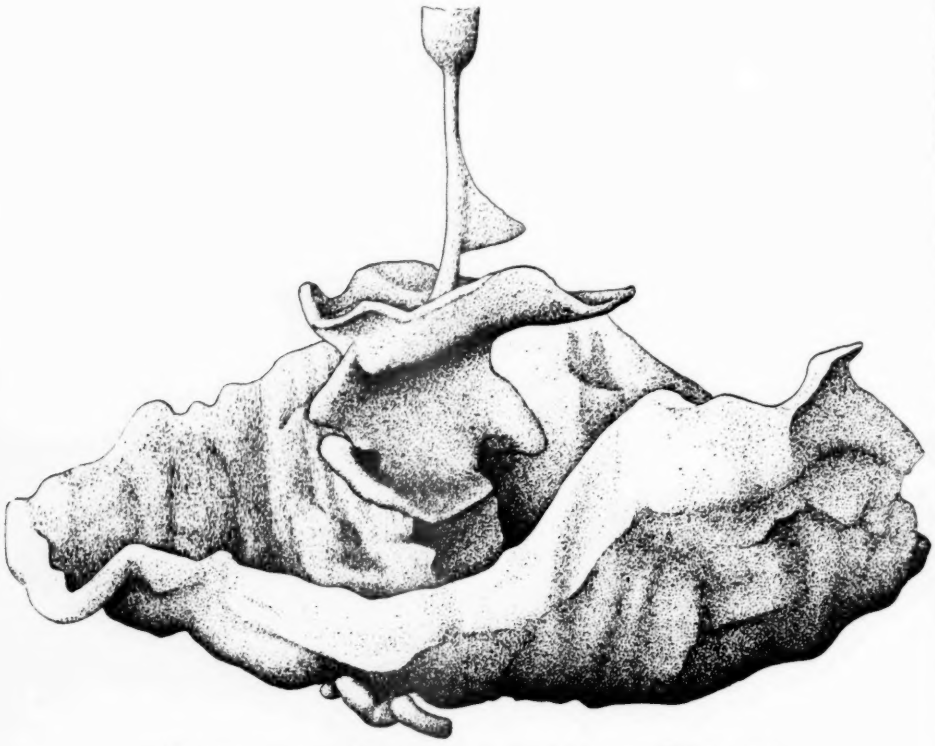


FIG. 60.—A wax model of a gland associated with an embryo in the late blastocyst stage, showing the unaltered fundus, the large, flat, and curved swollen segment, the spiral, and the rather long, straight neck opening in the embryo-chamber. × 75. Series 550.

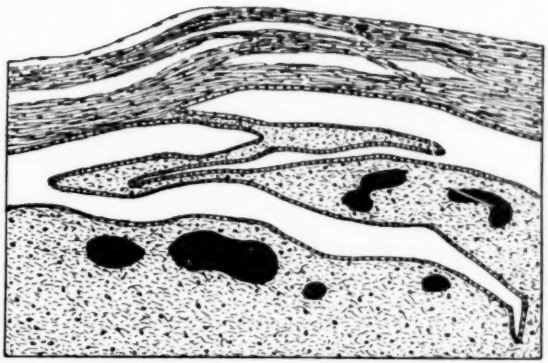


FIG. 61.—A still healthy septum between two adjacent glands in the decidua spongiosa, associated with an embryo in the primary amniotic cavity stage. The glandular epithelium covering the inner aspect of the muscularis is low. ×100 Series 599.

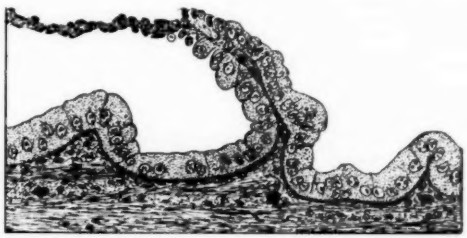


FIG. 62.—The destruction of the septa between the glands, associated with an embryo with 13 somites. Note the abrupt ending of the healthy epithelium and the high glandular epithelium covering the muscularis. ×200. Series 833.

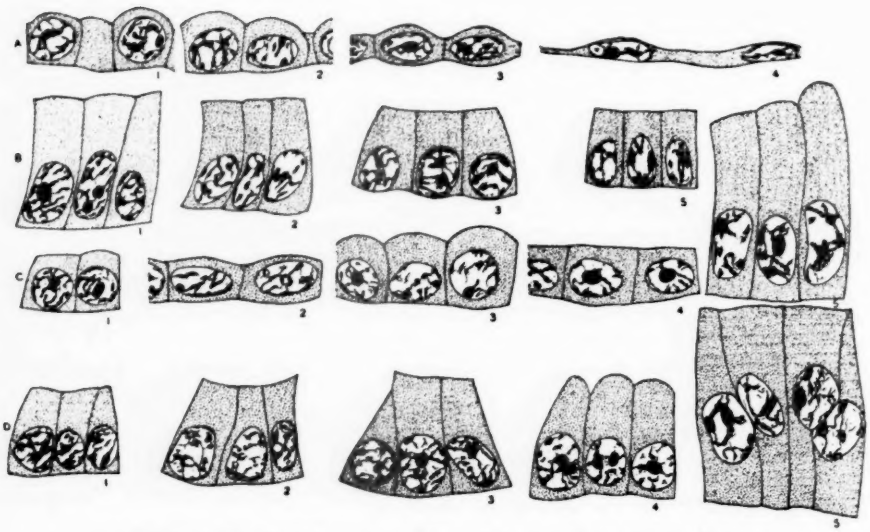
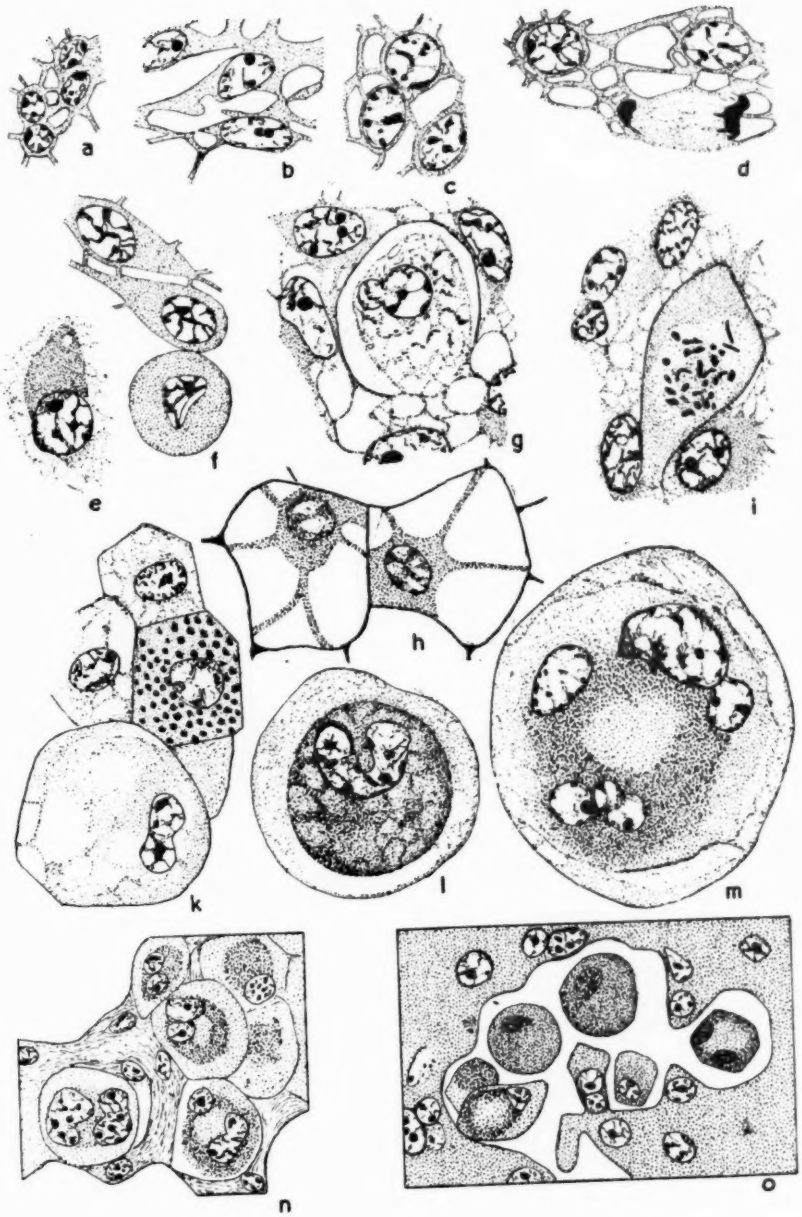


FIG. 63.—The epithelium of the glands: A, in the spiral section or the inner wall of the ballooned part; B, in the fundus; C, of the outer wall of the ballooned part covering the inner aspect of the muscularis; D, of an antimesometrial gland; 1, during the early blastula stage; 2, during the early primary amniotic cavity stage; 3, during the primitive streak stage; 4, when the embryo has 18 somites; 5, when the embryo is 12·5 mm. long. × 1000. Series 198, 222, 834, 754 and 601.

FIG. 64.—The changes taking place in the stromal and decidual cells: (*a*) stromal cells during anoestrus, all with small nuclei and vacuoles, series 496 (*cf.* fig. 2); (*b*) stromal cells during oestrus, all with large nuclei and large vacuoles, series 95 (*cf.* fig. 3); (*c*) cells during the dark stroma stage following oestrus, with large nuclei and small vacuoles, series 385 (*cf.* fig. 4); (*d*) pregnancy oedema, with large vacuoles, series 824 (*cf.* fig. 6); (*e, f*) early decidual reaction with pear-shaped cells and very early giant cell, series 36 (*cf.* fig. 9); (*g*) an early giant cell surrounded by pear-shaped stromal cells, series 222 (*cf.* fig. 10); (*h*) stromal cells with large vacuoles, prior to their destruction, embryo with 18 somites, series 754; (*i*) a young giant cell in mitotic division with numerous chromosomes, series 760; (*k*) a young giant cell and some stromal cells, one with coarse granules and two with vacuoles, series 834 (*cf.* fig. 14); (*l*) a young giant cell with irregular nucleus, dense inner cytoplasm and many vacuoles in the periphery, series 833; (*m*) a full-grown giant cell, with several nuclei, a clear central area, surrounded by a granular and a vacuolated peripheral zone, series 833 (*cf.* fig. 15); (*n*) part of the decidua spongiosa with many giant cells, series 833; (*o*) part of the ectoplacenta with the remains of detached giant cells in the maternal blood channels, series 833. *a–m*, × 1000; *n* and *o*, × 450.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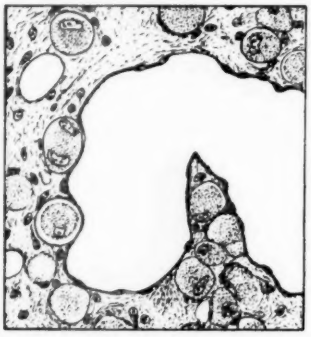

FIG. 65.—A decidual artery with endothelium and giant cells protruding in the lumen. ×200. Series 766.

FIG. 66.—A decidual artery in the decidua spongiosa; giant cells have entered the artery and line its wall. ×200. Series 754.

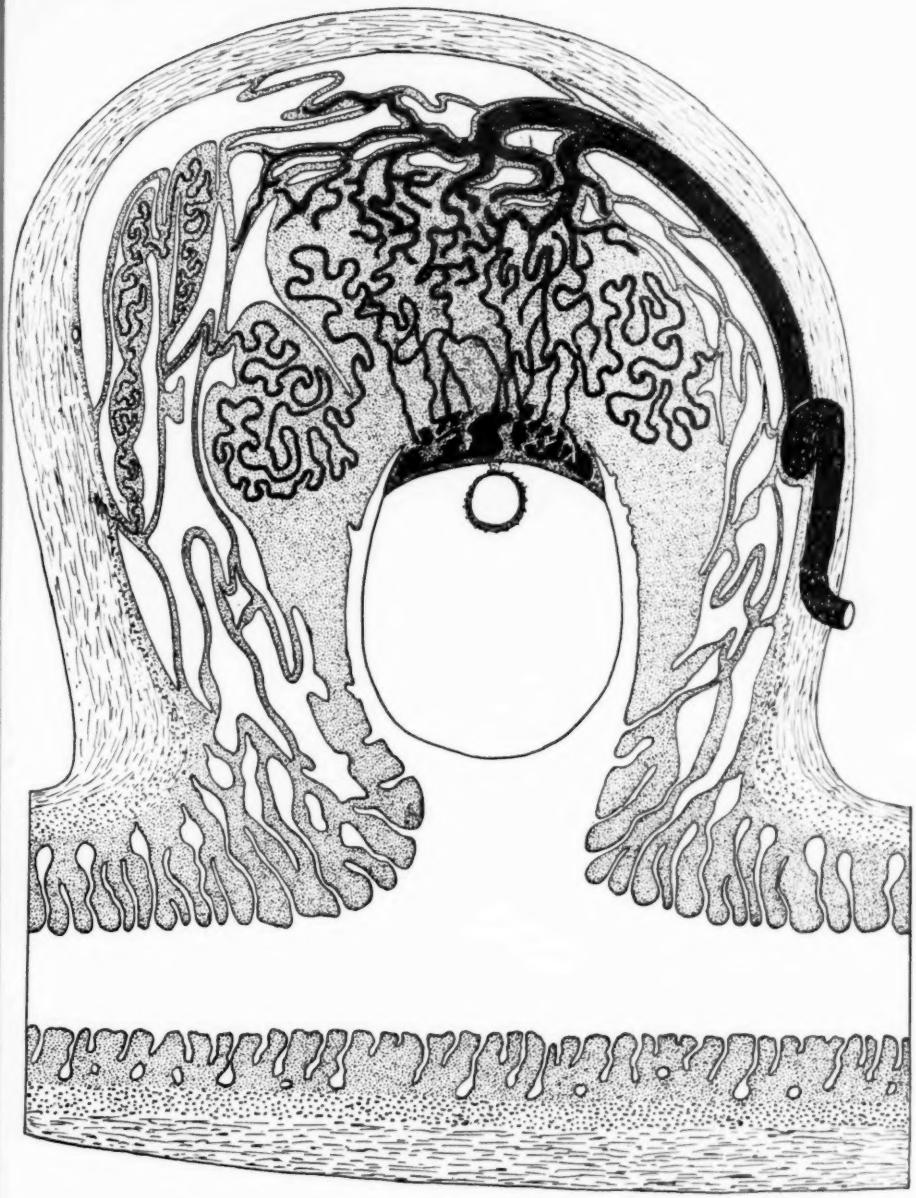

FIG. 67.—Schematic longitudinal section of the uterus, with an embryo in the primary amniotic cavity stage, to show the course of the decidual arteries and vein. To the left, a tiny arterial branch enters the decidua spongiosa from the muscularis, it swells up and follows its devious course in the decidua spongiosa, it swells again on entering the decidua compacta; the final straight portion of the artery enters the centre of the placenta in close proximity to a similar artery coming from the right. Several veins emerge from the periphery of the early placenta to join with numerous other branches and to form the single large decidual vein in the centre of decidua spongiosa; laterally this vein enters the muscularis and then the mesometrium.

FIG. 68.—A horizontal section of the uterine swelling with the embryo in the late primitive streak stage. The base of the placenta is surrounded by the decidua compacta. The coils of the three decidual arteries are arranged in fields separated by non-vascular areas. × 25. Series 559.

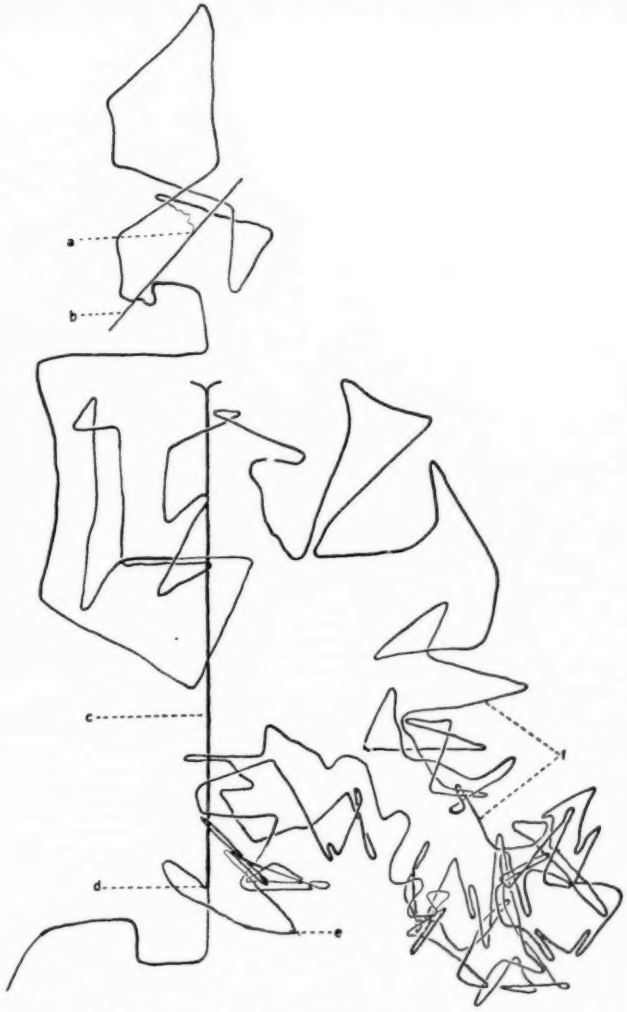

FIG. 69.—A projection on a tangential plane of a decidual artery, associated with an embryo with about 35 somites. *a*, The decidual artery branches off from a myometrial artery and enters the decidua spongiosa; *b*, myometrial artery; *c*, central placental artery; *d*, fusion of two decidual arteries; *e*, point where the decidual artery enters the already decomposed decidua compacta in which it follows a nearly straight course; *f*, coils of the artery in the decidua spongiosa. × 25. Series 69.

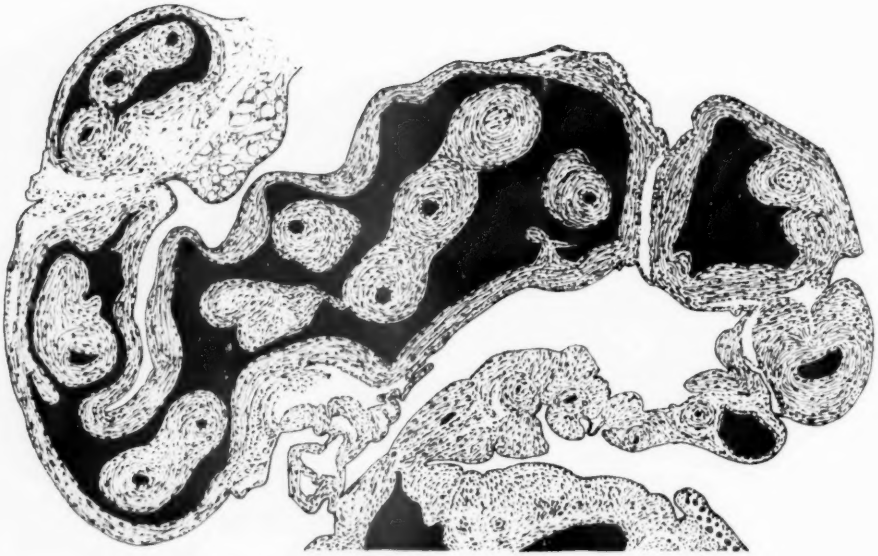

FIG. 70.—Portion of the mesometrium with the mesometrial artery twisting in the wide lumen of the vein. Animal going into anoestrus, after a recent post-partum ovulation. ×75. Series 979.

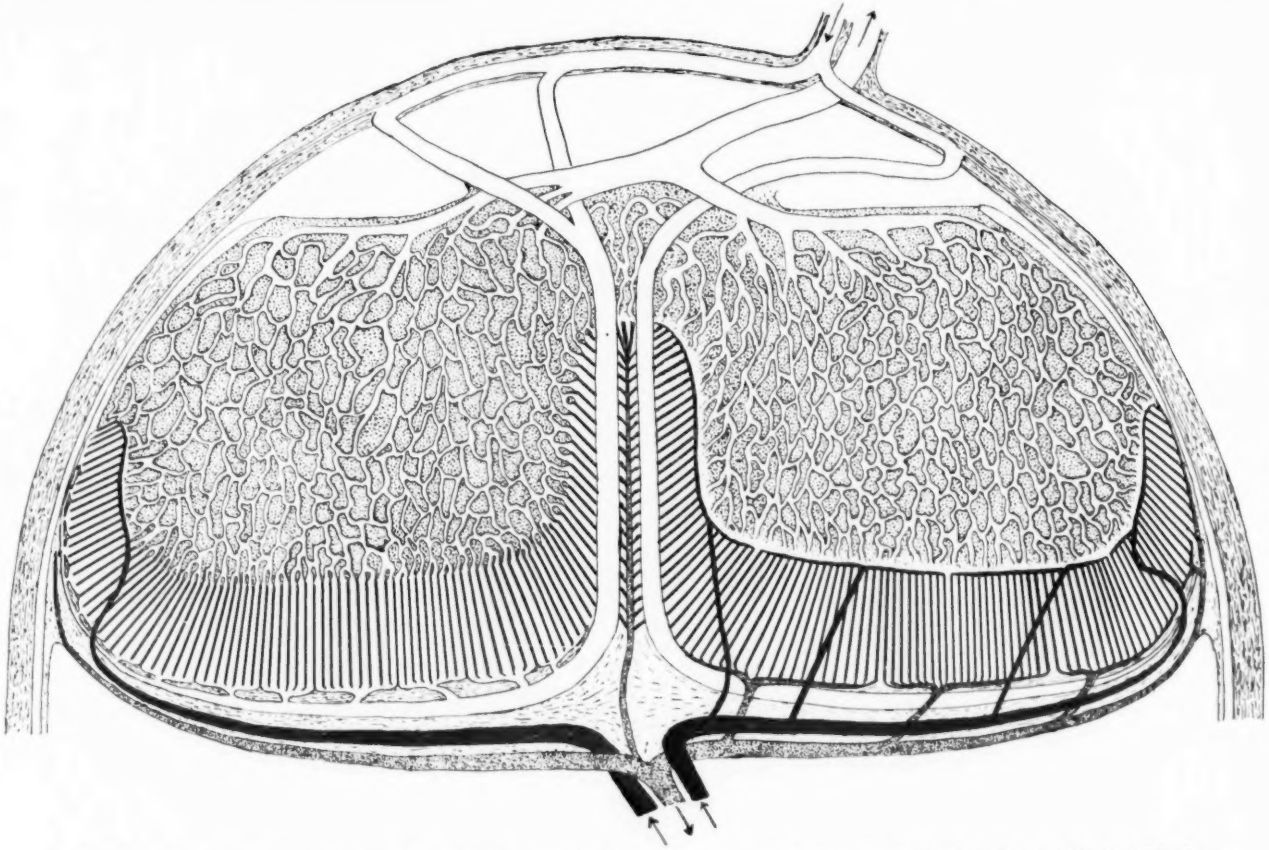

FIG. 71.—A schematic representation of the placental circulation during the later part of pregnancy (*cf.* fig. 21). In the right half of the figure the embryonic circulation is completely represented, the arteries in black and the veins darkly shaded, and the left half shows the maternal circulation.